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ERYTHRANTHE HOWALDIAE (SECT. *SIMIOLUS*; PHRYMACEAE), A NEW SPECIES FROM MONO CO., CALIFORNIA

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ABSTRACT

Erythranthe howaldiae Nesom, **sp. nov.**, is described from the Sierra Nevada of Mono Co., California, where it grows on a seepy, granite slope, known only from the type collection. It is at least superficially most similar to *E. percaulis* and *E. nudata*, both of which are serpentine endemics from northern California localities, but its closest evolutionary relationship may be with other species.

Collections and study by Ann Howald of the plants of Mono County, California, have brought to light a previously undescribed species of *Erythranthe* sect. *Simiolus*. The species is known only from the type locality, slightly east of Sonora Pass.

The observations here are similar to those of the collector, who recognized the close similarity of the Mono County plants to *Erythranthe percaulis* Nesom, which is endemic to serpentine habitats in the North Fork Feather River Canyon (Serpentine Canyon) of Plumas County, about 150 miles north of the Mono County locality (Schoenig 2016).

ERYTHRANTHE HOWALDIAE Nesom, **sp. nov.** **TYPE**: **California**. Mono Co.: Sierra Nevada east slope, Sonora Pass Road (Hwy 108), ca. 1.5 mi E of Sardine Meadow, N side of road, 38° 18' 34.2" N, 119° 34' 59.7" W, NAD 83, Pickel Meadow 7.5' Q. (T5N, R22E, S5), among mosses on gradual, S-facing, seepy granite slope, 8164 ft, uncommon annual herb, with high diversity of herbaceous plants, 24 Jul 2019, *A. Howald 5078* (holotype: CAS; isotype: PH).

Similar to *Erythranthe percaulis* in its annual duration, small and sessile cauline leaves, strictly ascending pedicels, and relatively small corollas but different in its geography and ecology, smaller stature, minutely hirsutulous leaves (adaxially) with slightly dilated, perfoliate bases, shorter fruiting pedicels, and larger corollas.

Annual herbs from shallow fibrous roots. **Stems** 1–4 from basal or near-basal nodes, erect to ascending from the base, 4–12 cm tall, glabrous or minutely stipitate-glandular at the nodes, terete, internodes 1.5–2.5 cm. **Leaves** basal and cauline, adaxial surfaces minutely hirsutulous with stiffly erect, sharp-pointed hairs, glabrous abaxially, basal and lowermost cauline petiolate, petioles 4–10 mm, blades ovate, 6–10 mm, margins shallowly serrate, more distal cauline abruptly becoming sessile, even-sized or becoming slightly smaller, oblong- to elliptic-ovate, entire, (mid to distal) mostly 4–6 mm long, base slightly dilated and perfoliate base. **Fruiting pedicels** 9–20 mm long, ascending. **Calyces** 5-lobed, in fruit cylindric to cylindric-obconic, 5–7 mm long, with sharply raised and purplish ridges and often sparsely purple-mottled near the ridges, lobes with acute to acute-acuminate apices, upper lobe slightly longer, the lower closing upward at maturity. **Flowers** in 3–6 pairs, from lowermost to uppermost nodes. **Corollas** yellow with a red spot in the center of the lower lip, palate ridges hairy, tube-throat narrowly cylindric-funnelform, 7–8 mm, exserted 3–4 mm beyond calyx margin, limb bilabiate, 3–5 mm in width (pressed). **Anthers** glabrous, included. **Styles** glabrous; stigma above the level of the anthers (apparently herkogamous). **Capsules** short-stipitate, included (capsule apex reaching calyx lobe sinuses).

Figure 1. *Erythranthe howaldiae*, from the holotype collection.

Figure 2. *Erythranthe howaldiae*, selected plants from the array in Figure 1.

Figure 3. *Erythranthe howaldiae*, flower details from plants of holotype collection.

Figure 4. *Erythranthe howaldiae*, leaf details from plants of holotype collection.

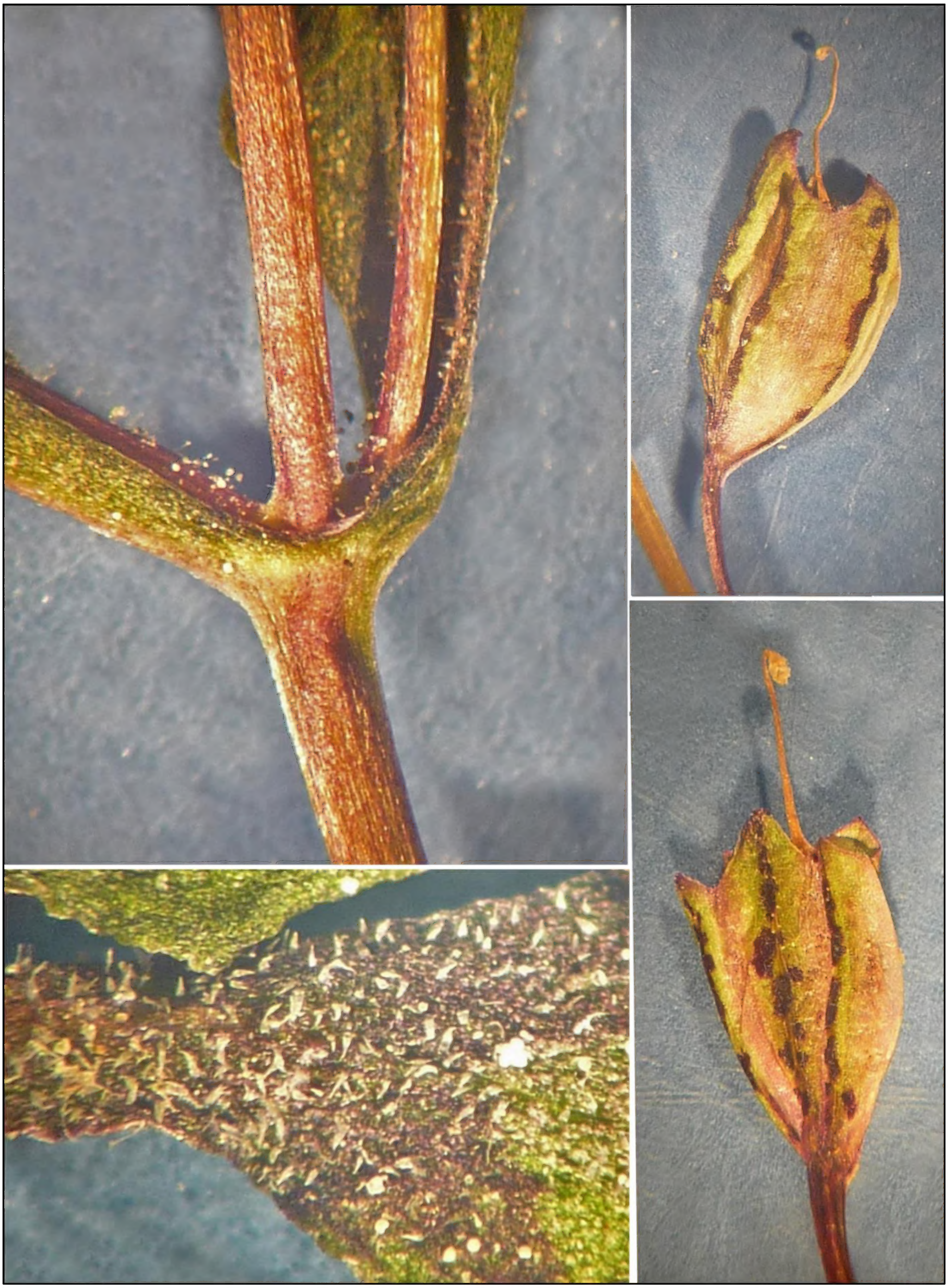

Figure 5. *Erythranthe howaldiae*, details from plants of isotype collection. Bottom left shows vestiture of adaxial leaf surface.

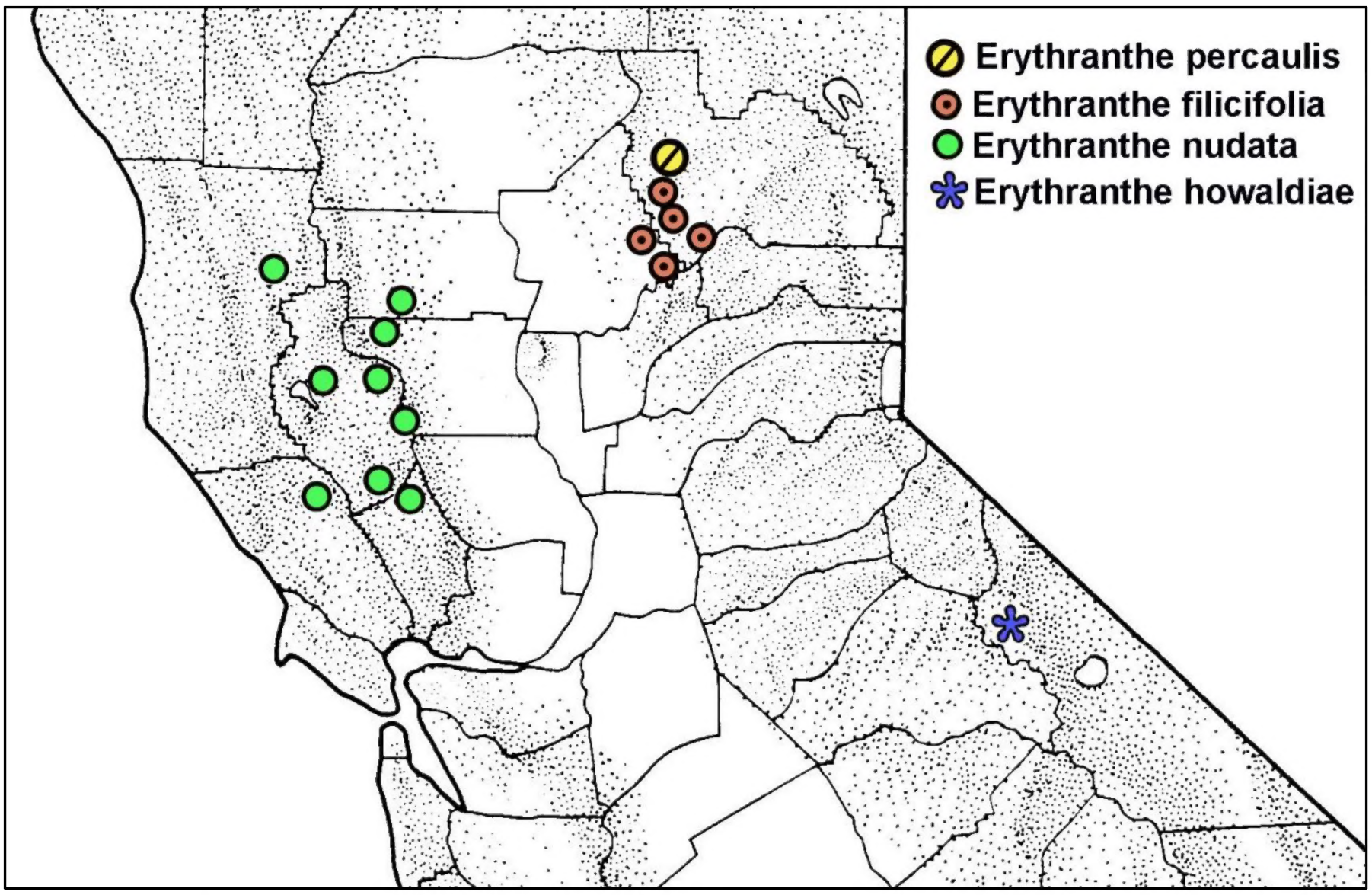

Figure 5. Distribution of *Erythranthe howaldiae* and putative close relatives. See Keever et al. (2016) for details on the distribution of *E. filicifolia*.

Figure 6. Locality of *Erythranthe howaldiae* type collection — south-facing, seepy granite slope on north side of Hwy 108 in Mono County. Leavitt Creek is along the south side of the road. Google Earth photo.

The species is named for its collector, Ann Howald, who has been studying the Mono County flora since 1975 and working toward an annotated checklist. She has an MA in Botany from UC-Santa Barbara and has been a consulting botanist focusing on rare plant surveys and conservation issues. She's now retired and an active volunteer for the California Native Plant Society, living in Mono County in the summer and teaching about its plants and habitats.

Erythranthe howaldiae is closely similar in aspect to *E. percaulis* and *E. nudata* (Curran ex Greene) Nesom, especially to the former. As in *E. percaulis*, the distinctly exserted style and stigma and the herkogamous arrangement of stigma and anthers indicate that flowers of *E. howaldiae* are chasmogamous and allogamous. The morphological differences, however, are consistent and the taxa are separated in geography (Fig. 5) and ecology (Fig. 6).

1. Cauline leaf blades 5–15(–30) mm; plants glabrous or stems, leaves, and fruiting calyces minutely stipitate-glandular, hairs 0.05–0.1 mm, at least just above nodes; fruiting calyces 6–13 mm long; corolla limb expanded 8–12 mm in width; serpentine substrate ..... **Erythranthe nudata**
1. Cauline leaf blades 4–10 mm; plants glabrous; fruiting calyces 4–7 mm long; corolla limb expanded 3–5 mm in width; serpentine or granite substrate.
    2. Stems 7–30 cm tall, internodes 2–5 cm; leaves glabrous on both surfaces; corolla tube-throat 4–6 mm long, exserted 2–3 mm beyond the calyx, throat floor and lower lip with red markings; fruiting pedicels 15–35 mm long; serpentine substrate ..... **Erythranthe percaulis**
    2. Stems 4–12 cm tall, internodes 1.5–2.5 cm; leaves minutely hirsutulous adaxially; corolla tube-throat 7–8 mm long, exserted 3–4 mm beyond the calyx, lower lip with a single red spot; fruiting pedicels 9–20 mm long; granite substrate ..... **Erythranthe howaldiae**

The similarities also suggests that *Erythranthe howaldiae* is part of the evolutionary clade hypothesized to include *E. percaulis*, *E. nudata*, and *E. filicifolia* (Sexton et al.) Nesom (e.g., Nesom 2013a, 2013b, 2019), perhaps as a derivative of *E. percaulis* (or of *E. nudata*), with a loss of fidelity to serpentine substrate. On the other hand, the hirsutulous leaf surfaces and unusual leaf bases of *E. howaldiae* suggest that its evolutionary affinity may be closer to the group of annual species comprising *E. microphylla*, *E. nasuta*, *E. laciniata*, *E. marmorata*, and *E. pardalis* (Nesom 2019), the latter three more similar in geography to *E. howaldiae*.

ACKNOWLEDGEMENTS

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OHIO FLORA: ADDITIONS, NOTEWORTHY FINDS, AND DELETIONS

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ABSTRACT

Additions to the species list for the flora of Ohio are presented, based upon reports vouchered by herbarium specimens. Included are seven new genera and 49 new species and subspecies, representing 10 families. Of these, the following genera are first reports for the state: *Calibrachoa*, *Callicarpa*, *Cyclospermum*, *Dittrichia*, *Hippophae*, *Photinia*, and *Sideritis*. None of the discoveries included in this work represents a new family for Ohio. Also included are noteworthy finds and discussions of taxa deleted from the flora and from county records, along with our rationale for each change.

As is the case in many other Midwestern states, the Ohio flora is continuing to expand as new treatments are published and new discoveries are made. In the last comprehensive catalog of the flora of Ohio, Cooperrider et al. (2001) listed 2,998 taxa, including species, major infraspecific taxa, and interspecific hybrids. Of this total, 979 (23 percent) are not native to the state. Vincent et al. (2011) added 80 new taxa of native and introduced vascular plants to this ever-growing list, and now, following an additional eight years of survey work, as well as examination of numerous herbarium sheets of previously unrecorded or recently recognized species once lumped in synonymy, we present another 66 taxa to include in the Ohio flora.

While additions to the state's flora and other significant finds are important to record as vouchers and in peer-reviewed articles, so too is making known any necessary deletions that result from new information or application of higher inclusion standards. In many cases, this means verifying key characters from flowering and non-flowering material necessary for positive identification of specimens, or at the very least, from label information which includes details of such characteristics of the given plant not revealed on the voucher itself.

In this paper, we not only list new and noteworthy finds from Ohio (Section I), but also present a list of historical state and county records (Section II) deleted on the basis of our efforts to verify specimens used in support of existing published and online reports. The additions and deletions referenced in this work represent the latest effort to record and maintain an accurate, up-to-date catalog of the dynamic flora of Ohio, a moving target in no small part due to climate change, habitat creation, site alteration, and other anthropogenic forces (Vincent et al. 2011).

Methods

Field surveys were conducted throughout Ohio with collections included made by numerous botanists and naturalists along with additional specimens found through our examination of holdings from 21 herbaria, including BGSU, BH, BHO, BUT, CINC, CLM, CM, DAWES, ISC, KE, MICH, MIL, MIN, MO, MU, NCU, NY, OS, SWF, UWO, and YUO (acronyms from Thiers [continuously updated]). State and county deletions found in Section II are based on determinations made by the authors and/or the Ohio Rare Plant Advisory Committee at biennial meetings since 2002.

All taxa included here are documented by herbarium specimens with material sufficient for positive identification. Because some specimens fell short of meeting this standard, many *Crataegus* and *Rubus* specimens examined in preparation for this article were omitted or are cited only in passing. To ensure that sufficient material was available for proper identification (especially for *Crataegus*, *Prunus*, and *Rubus*), multiple sheets were often collected to capture the range of variability within populations, as well as to document flowering and fruiting characteristics. For this reason, where vouchers include multiple sheets, the total number of duplicates corresponding to a given collection is indicated next to the corresponding herbarium code. Furthermore, it should be noted that information presented herein was taken directly from specimen labels created by many different botanists dating back to the late 19th century; for this reason, some inconsistencies occur. For each voucher cited, whenever possible, the authors have included the following label information: township, section, short description of site or habitat where plant was found, town or specific location where collected, date collected, collector's last name, and personal collection number, and, in parentheses, the herbarium where each specimen is deposited.

Section I. Additions and noteworthy finds

1) ***AMBROSIA BIDENTATA*** Michx. × ***AMBROSIA ARTEMISIIFOLIA*** L. (Asteraceae) – hybrid ragweed. **Pike Co.**: Newton Twp., one mature, sparsely-fruiting plant observed growing amongst both parent species on dry, disturbed/scraped, open, W-facing (hilltop) embankment, 5 Sep 2012, *Riley 2191* (OS).

This naturally occurring, unnamed hybrid has not previously been reported, though other hybrid ragweeds have been recognized (Strother 2006). Because of the rarity of this hybrid, we do not propose a binomial.

2) ***AMELANCHIER HUMILIS*** Wiegand (Rosaceae) – low serviceberry. **Lucas Co.**: Holland, 5 May 1934, *Thomas & Campbell s.n.* (OS); Swanton Twp., section 21, shrubs, about 1-1.5 m tall, sandy bank at edge of oak woods, Oak Openings Park, 25 Apr 1976, *Cusick s.n.* (KE); colonial shrub 1 m tall, Oak Openings Park, 3 Jun 1987, *Cusick 26494 & Denny* (OS); Spencer Twp., section 35, locally common species along trail on dry, sandy site along utility line clearing, 26 Aug 2006, *Riley 354* (OS); *ibid*, 30 Jun 2012, *Riley 2193 & Boone* (OS), *2194* (MU), *2195* (CLM).

Amelanchier humilis is distinct due to its strongly rhizomatous growth habit forming scattered colonies (Campbell et al. 2014). This characteristic is most certainly evident in populations found within Ohio's Oak Openings Region where it occurs exclusively in dry, sandy soil. Campbell et al. (2014) reported the distribution of this wide-ranging species to include Manitoba, Ontario, Quebec, Saskatchewan, and 18 states including Ohio. In Michigan, *Amelanchier humilis* is treated as conspecific with *Amelanchier sanguinea* (Pursh) DC and *Amelanchier spicata* (Lam.) K. Koch, as it shares characters of both species complexes (Michigan Flora Online 2019).

3) ***AMELANCHIER INTERIOR*** E.L. Nielsen (Rosaceae) – inland serviceberry. **Erie Co.**: Kelleys Island, Long Point, Monagan Rd., north of Camp Patmos, 17 May 2013, *Cusick 37704 & Hayes* (MU). **Lucas Co.**: Spencer Twp., section 35, rare, one fruiting, arborescent shrub growing in dry, sandy soil along edge of mature oak woods, Holland, 26 Jun 2012, *Riley 2196-2197 & Boone* (OS), *2198* (CLM), *2199* (MU); *ibid*, 23 Jul 2016, *Riley 3384* (KE), *3385* (CLM).

There are three earlier specimens of this taxon from Erie County, two at OS and one at KE: the first collection was made at Cedar Point on 28 Jun 1915, *Grover s.n.* (OS), while the latter two were found at Kelleys Island on 21 Apr 1977, *Cusick s.n.* (KE), and on 12 May 1988, *Cusick 27356* (OS). At the time of its rediscovery in 2012, this species was considered extirpated from Ohio (ODNR 2018).

4) ***ANAGALLIS MINIMA*** (L.) E.H. Krause (Primulaceae) – chaffweed. **Gallia Co.**: Greenfield Twp., section 16, rare, small, local population growing under oak canopy, Gallia, 3 Jun 2017, *Riley 3712* (OS). **Pickaway Co.**: Wayne Twp., locally abundant in and around open, shallow, seasonally wet depressions on edge of fallow field, Circleville, 21 May 2012, *Riley 2204* (OS); Wayne Twp., 100s of plants in low areas along edge of fields and swales, Wildlife Production Area, 22 May 2012, *Gardner 7193 & Riley* (OS); Harrison Twp., section 1, small, local population growing on recently disturbed, sparsely vegetated, seasonally wet, open site, Teays Valley East Middle School, Ashville, 24 Jun 2012, *Riley 2205* (OS), *2206* (MU). **Pike Co.**: Jackson Twp., section 10, locally scattered population growing within small canopy opening on dry, upland (ridgetop) site, Beaver, 9 Jun 2018, *Riley 4056* (OS); Camp Creek Twp., extremely large population growing on semi-shaded site at edge of lawn and adjacent mesic woods, Lucasville, 22 Jun 2018, *Riley 4057* (OS), *4058* (KE); *ibid*, 15 Jun 2019, *Riley 4273* (CM). **Ross Co.**: NE ¼ Jefferson Twp., rare, two plants found growing around edge of small, wet, tire rut depression on N central side of recently clear-cut riparian/floodplain forest, 3 Jun 2012, *Riley 2207* (OS – photograph only). **Scioto Co.**: Madison Twp., section 25, small, local population growing in open, rather sparsely vegetated site at gravesite, Minford, 3 Jun 2017, *Riley 3713* (OS); S-SW Washington Twp., very local and relatively small population growing within sparsely vegetated, semi-shaded lawn, 24 Jun 2017, *Riley 3714* (OS); central Nile Twp., locally abundant, growing in open, sparsely vegetated, shallow (tire-rut) depressions along bridle trail, Shawnee State Forest, 24 Jun 2017, *Riley 3715* (OS), *3716* (KE); S-SW Union Twp., very local population growing within dry, somewhat open, upland (ridgetop) mature oak forest community, Shawnee State Forest, 9 Jun 2018, *Riley 4059* (OS); extreme western Morgan Twp., very small and local but healthy and robust population growing on sparsely vegetated, shaded – mostly shaded site, 22 Jun 2018, *Riley 4060* (OS).

Historical collections of this species, housed at OS, were made in Jackson and Ross counties by Floyd Bartley in 1935. At the time this species was rediscovered in Pickaway County in 2012 by Riley, it was listed as presumed extirpated in Ohio, since it had not been reported for 77 years (ODNR 2018). Collections from Gallia, Pike, Ross, and Scioto counties represent new county records for this elfin annual. Riley also observed this species in Jackson County in 2018, though no vouchers were made.

5) ***ARISTIDA BASIRAMEA*** Engelm. ex Vasey (Poaceae) – forked three-awn. **Lucas Co.**: Swanton Twp., sections 28 & 29, sloped dune barren, about 10-15% coverage, area periodically burned, Oak Openings Preserve, 20 Sep 1996, *Walters 1996:198 & Jacksy* (CLM); Swanton Twp., dry sand

savanna, Badger Barrens, Oak Openings Preserve MetroPark, 24 Aug 2012, *Gehring & Klavins s.n.* (MICH).

This species occurs on dry, sandy ground in 22 counties throughout Michigan's lower peninsula and in Delta and Schoolcraft Counties in the state's upper peninsula (Michigan Flora Online 2019). A duplicate of *Walters 1996:198* is housed in the collection of Metroparks Toledo.

6) ***CALIBRACHOA PARVIFLORA*** (Juss.) D'Arcy (Solanaceae) – seaside petunia. **Greene Co.**: Ramp off Interstate 675 southbound to Dayton Yellow Springs Road, gravelly edge of road, 30 Jun 2018, *Boone s.n.* (MU). **Hamilton Co.**: Mud flat of Great Miami River, Shawnee Lookout, 20 Oct 2015, *Boone s.n.* (MU); Miami Township Community Park, sandy, rocky and muddy flats of Great Miami River, 28 May 2018, *Boone s.n.* (CINC, MU).

Calibrachoa parviflora is native to the southwestern United States, Mexico, and South America (Jepson Flora Project 2019). USDA NRCS (2019) reported collections from 15 states, ranging from the Pacific coast to the Atlantic seaboard, with most occurrences located in the southern half of the continental United States. The BONAP website (Kartesz 2015) lists the species for 18 states, where it is listed as native to Arizona, California, and Utah and as introduced in fifteen other states.

7) ***CALLICARPA DICHOTOMA*** (Lour.) K. Koch (Lamiaceae) – purple beautyberry. **Licking Co.**: Growing in full shade, east side, SW of Boy Scout Pond area, The Dawes Arboretum, 7 Sep 2017, *Dixon s.n.* (DAWES). **Wayne Co.**: Escaped from cultivation, 1917, *Anonymous s.n.* (OS).

Callicarpa dichotoma is an ornamental shrub up occasionally planted for its attractive pink or white flowers, as well as for its equally attractive fruits (drupes) which at maturity are purple or, in the case of f. *albifructa* T. Yamaz., white. The escaped Licking County collection cited here is f. *albifructa*. Beautyberry is native to China and Korea (Rehder 1947), and was first introduced into cultivation in 1857. Kartesz (2015) reported escaped collections from eight states, including Alabama, Arkansas, Delaware, Missouri, North Carolina, Pennsylvania, South Carolina, and Virginia, while USDA NRCS (2019) reported collections from only six states, including Kentucky and Tennessee.

8) ***CAREX ALBICANS*** Willd. ex Spreng. var. ***ALBICANS*** × ***CAREX UMBELLATA*** Schkuhr ex Willd. (Cyperaceae) – hybrid sedge. **Cuyahoga Co.**: Upland immediately west of Rocky River, Rocky River Reservation, North Olmsted, 14 May 1999, *Wilder & McCombs 10743* (MICH).

The only specimen of this hybrid known from Ohio was determined by Dr. A.A. Reznicek in 2007. On this voucher, Dr. Reznicek notes that the plant is sterile and that the anthers are not exerted, and that the basal spikes, small perigynia, and thin culms are further evidence of this interspecific hybrid.

9) ***CAREX FLACCA*** Schreb. (Cyperaceae) – glaucous creeping sedge. **Portage Co.**: Charlestown Twp., rather large, local, colonial population dominant within open, moist, shallow depression surrounded by successional woods, Camp Ravenna Joint Military Training Center, Ravenna, 27 Feb 2018, *Riley 4040* (OS – three sheets); *ibid*, 5 Jun 2018, *Riley 4074* (OS), *4075* (KE – two sheets), *4076* (MICH); *ibid*, 14 Jun 2018, *Riley 4077* (OS), *4078* (KE), *4079* (CLM), *4080* (CM).

The origin of this population is a bit of a mystery given that *Carex flacca* typically occurs in calcareous soils throughout Europe (Ball & Reznicek 2002), the likes of which do not occur at this site. Ball & Reznicek (2002) reported this species as being introduced in the lower Great Lakes region, including Ontario, Quebec, Michigan, and New York. In Ohio, this rather attractive species was discovered at a location somewhat removed from the nearest homesite, which predates 1940 when the US Government purchased the land from private citizens to establish the Ravenna Army Ammunition Plant (renamed Camp James A. Garfield Joint Military Training Center in October 2018). Until recently, this species was not widely available in the nursery industry or horticultural trade. Due to the size of this population, it is likely that it has been established at this site for a considerable time.

10) ***CAREX FORMOSA*** Dewey (Cyperaceae) – handsome sedge. **Portage Co.**: Charlestown Twp., rare, in meadow at edge of young woods, Camp Ravenna Joint Military Training Center, Ravenna, 2 Jun 2010, *Gardner 6920* (OS, MICH).

Carex formosa was first collected in Ohio in Wood County in 1958 [*Easterly 531* (OS)]. Prior to its 2010 rediscovery, this sedge was presumed extirpated in Ohio, since it had not been observed in the state for more than 20 years, but is currently listed as State Endangered (ODNR 2018).

11) ***CAREX HAYDENII*** Dewey (Cyperaceae) – Hayden's sedge. **Cuyahoga Co.**: 10-15 clumps in gently sloping, wet meadow; mistakenly introduced as *Carex stricta* during wetland restoration activities in 2009 or 2010, South Chagrin Reservation, 21 May 2018, *Reinier 1199* (Herbarium of Cleveland Metroparks); *ibid*, 1 Jun 2018, *Reinier 1211* (KE).

The Cuyahoga County collections of this species, verified by Dr. A.A. Reznicek, were gathered from a naturalized planting at a wetland restoration site rather than from a naturally occurring population. All other Ohio records cited in Braun (1967) and Kartesz (2015) were found to be misidentified. See species entry in Section II for details concerning these recently annotated specimens.

12) ***CAREX LUPULINA*** Muhl. ex Willd. × ***CAREX LURIDA*** Wahlenb. (Cyperaceae) – hybrid sedge. **Portage Co.**: NW ¼ Paris Twp., four local plants observed growing within shaded swamp woods, Camp Ravenna Joint Military Training Center, 8 Jul 2016, *Riley 3414* (OS), *3415* (MICH); *ibid*, 13 Jul 2016, *Riley 3416* (KE); NE ¼ Paris Twp., one or two robust plants observed growing next to large *Salix sericea* shrub on E edge of open wetland, Camp Ravenna Joint Military Training Center, 23 Aug 2016, *Riley 3417* (OS); *ibid*, 7 Aug 2017, *Riley 3782* (CLM), *3783* (CM). **Trumbull Co.**: Braceville Twp., south shore of beaver pond, robust form, 15 Jul 1945, *Rood s.n.* (YUO).

ODNR Chief Botanist Richard L. Gardner (pers. comm.) informed us that this hybrid was collected Ashtabula County by Ms. Kashmira Asnani. Her specimen will be housed at OS.

13) ***CAREX OKLAHOMENSIS*** Mack. (Cyperaceae) – Oklahoma sedge. **Cuyahoga Co.**: Hundreds of fruiting culms in routinely mowed powerline corridor, Middleburg Heights, 16 Jun 2014, *Reinier 305* (CLM); *ibid*, 23 Jun 2014, *Reinier 313* (OS).

Carex oklahomensis is native to the southern and southeastern states. According to Kartesz (2015), the closest populations to Ohio are within the Mississippi Embayment physiographic region of

western Kentucky, which are considered native (Jones 2005), and two counties in southwestern Indiana (Daviess and Posey), which are considered to be introduced. Jones (2005) mentioned "wet woodlands and meadows" as habitats for this species.

14) ***CAREX SYLVATICA*** Huds. (Cyperaceae) – European woodland sedge. **Portage Co.**: Charlestown Twp., locally common species growing in young, mesic woods and in open grass/roadside strip, Camp Ravenna Joint Military Training Center, 21 May 2015, *Riley 3118* (OS), *3119* (KE); *ibid*, 26 May 2015, *Riley 3120* (OS), *3121* (MICH); *ibid*, 2 Jun 2015, *Riley 3122* (OS), *3123* (CLM); *ibid*, 9 Jun 2015, *Riley 3124* (CM), *3125* (MU); *ibid*, 1 Jun 2016, *Riley 3433* (OS), *3434* (CM), *3435* (MICH); *ibid*, 6 Jun 2016, *Riley 3436* (OS), *3437* (MU).

Although this Old World sedge has been reported from eastern North America (Ball & Reznicek 2002), it was not previously known from Ohio. The origin of this population, located not far from an old homesite predating 1940, is unknown, since this species has not been widely used in horticulture until recently. It is just as conceivable that this population was an accidental introduction as it is to believe that it was deliberately planted here 80 or more years ago.

15) ***CAREX VIRIDISTELLATA*** Derieg, Reznicek, & Bruederle (Cyperaceae) – greenstar sedge. Confirmed collections of this recently described species from **Adams, Greene, Seneca,** and **Wyandot Counties** are cited in Derieg et al. (2013). Additional collection: **Champaign Co.**: Concord Twp., section 11, infrequent in narrow cinquefoil-sedge fen, 11 Jun 2013, *Gardner 7236, Gibson, & Schneider* (OS).

16) ***CARYA GLABRA*** (Mill.) Sweet var. ***MEGACARPA*** (Sarg.) Sarg. (Juglandaceae) – pignut hickory. **Portage Co.**: SE ¼ Windham Twp., one mature, double-stemmed tree growing at S-SW corner of mature, dry, upland white oak woods growing in shallow soil over sandstone bedrock, Camp Ravenna Joint Military Training Center, 29 Sep 2015, *Riley 3130* (OS), *3131* (KE).

This uncommon variety is recognized by its larger leaflets and fruit 2.5-5 cm long with husks 3.5 mm thick. The range of this variety extends from New York to southern Illinois, south to southern Florida, Alabama, and Louisiana (Fernald 1950).

17) ***CARYA OVATA*** (Mill.) K. Koch var. ***NUTTALLII*** Sarg. (Juglandaceae) – small-fruited shagbark hickory. **Portage Co.**: NE ¼ Brimfield Twp., uncommon, one declining tree from original woodland growing on dry site, Lions Community Park, Brimfield, 27 Sep 2015, *Riley 3134* (OS), *3135* (KE), *3136* (MU).

Fernald (1950) distinguished this variety by its small, subglobose nut that is strongly compressed laterally and only 1.5-2 cm long. Its known distribution spans from Massachusetts and Pennsylvania west to Missouri.

18) ***CASTANEA MOLLISSIMA*** Blume (Fagaceae) – Chinese chestnut. **Franklin Co.**: Madison Twp., section 35, few locally escaped seedlings and saplings originating from nearby planted parent trees, Columbus, 31 Aug 2013, *Riley 2643* (OS), *2644* (BHO), *2645* (MU), *2646* (CLM). **Portage Co.**: extreme central Charlestown Twp., uncommon, one locally escaped sapling growing on W edge of mesic woods, Camp Ravenna Joint Military Training Center, 6 Sep 2017, *Riley 3787* (OS), *3788* (KE).

This species has been widely planted throughout the United States for the last century. Chinese chestnuts have long been produced commercially in Carroll County (Route 9 Cooperative 2019). Escapes of this species are typically local and limited to a few individuals at most, such as the case for both of these populations.

19) ***CRATAEGUS COCCINIOIDES*** Scheele (Rosaceae) – Kansas hawthorn. **Mahoning Co.**: NW ¼ Milton Twp., several flowering trees growing on dry slope on N side of Lake Milton tributary at public fishing access site, Lake Milton Public Hunting and Fishing Area, 19 Jul 2014, *Riley 2931* (OS); *ibid*, 5 May 2016, *Riley 3467* (OS), *3468* (KE), *3469* (UWO); *ibid*, 28 Apr 2017, *Riley 3801* (CM – two sheets). **Portage Co.**: NE ¼ Edinburg Twp., locally common, small trees with platy bark scattered along fencerow and within low, well-drained successional woods on open, mesic site, West Branch Wildlife Area, 12 May 2015, *Riley 3150* (UWO); *ibid*, 8 May 2016, *Riley 3470* (OS), *3471* (KE), *3472* (UWO); NE ¼ Edinburg Twp., mature trees growing along fencerow on N-NW side of grassy trail and on N side of pond, West Branch Wildlife Area, 8 May 2016, *Riley 3473* (OS), *3474* (UWO); NE ¼ Paris Twp., uncommon, two trees growing on W edge of mesic woods, Camp Ravenna Joint Military Training Center, 12 May 2016, *Riley 3475* (OS), *3476* (KE), *3477* (UWO); NE ¼ Paris Twp., one of five mature trees counted and several saplings observed growing on rich, loam soil on edge of young woods, Camp Ravenna Joint Military Training Center, 26 Apr 2017, *Riley 3802* (OS), *3803* (KE), *3804* (CLM). **Summit Co.**: single tree growing along north wooded fence line, Stow Armory, Stow, 26 Apr 2017, *Riley 3805* (OS), *3806* (KE). **Trumbull Co.**: SW ¼ Newton Twp., two small trees observed growing on S edge of rich, mesic woods, Pricetown UM Church, Newton Falls, 28 Apr 2017, *Riley 3807* (OS); SW ¼ Newton Twp., one healthy, medium-size, double-stemmed tree with others in the area growing on S side of ditch and on S edge of narrow woodlot, Newton Falls, 28 Apr 2017, *Riley 3808* (OS), *3809* (KE).

Based on Lance (2014), a few specimens are var. *dilatata* (Sarg.) Eggleston, in which the anthers are pink-light purple instead of cream or off-white as in the typical variety. Phipps (2014) treated this variant as a synonym of the species, while Lance (2014) recognized it as distinct. Lance stated that the typical variety does not occur in Ohio, while var. *dilatata* occurs throughout the southeast quarter of the state. Of the specimens cited above (most of which include flowers), var. *dilatata* has only been collected in the northeast quarter, at West Branch Wildlife Area in Portage County.

20) ***CRATAEGUS COMPACTA*** Sargent (Rosaceae) – Thames hawthorn, clustered hawthorn. **Portage Co.**: Edinburg Twp., rare, one of two mature, fruiting trees located on E side of gravel access lane leading south from parking area to ag field, West Branch State Wildlife Area, 13 Jun 2017, *Riley 3810* (OS), *3811* (KE), *3812* (UWO); *ibid*, 17 Jun 2017, *Riley 3813* (UWO); *ibid*, 8 Jul 2017, *Riley 3814* (UWO – two sheets); *ibid*, 20 May 2018, *Riley 4104* (OS – two sheets), *4105* (KE); *ibid*, 24 May 2018, *Riley 4106* (OS – two sheets), 4107 (KE); *ibid*; 4 Aug 2019, *Riley 4274* (CLM), *4275* (CM), *4276* (MICH), *4277* (MU); Edinburg Twp., rare, one double-stem tree with non-glaucous pomes growing on S edge of mesic woods, West Branch State Wildlife Area, 4 Aug 2019, *Riley 4278* (OS), *4279* (KE). **Trumbull Co.**: Vernon Twp., one healthy tree with non-glaucous pomes growing on edge of mesic to moist-mesic successional woods (thicket) at W end of open meadow, Shenango State Wildlife Area, 31 Aug 2019, *Riley 4280* (OS – two sheets), *4281* (KE).

According to Lance (2014), *Crataegus compacta* "is today known to occur sporadically in the U.S. from Michigan to Pennsylvania with rare appearances in Ohio and the Virginias." *Crataegus compacta* was described in 1907 from London, Ontario, approximately 210 km (130 miles) north of the Portage County populations and approximately 188 km (117 miles) north of the Trumbull County population cited above, all of which occur at the southern edge of its range.

21) ***CRATAEGUS PENNSYLVANICA*** Ashe (Rosaceae) – Pennsylvania hawthorn. **Portage Co.**: Paris Twp., rare, locally scattered, mature, heavily fruiting trees growing near and along south edge of rich, mesic woods & red pine plantation, Camp Ravenna Joint Military Training Center, 11 May 2015, *Riley 3156* (OS), *3157* (CM), *3158* (UWO); *ibid*, 12 May 2015, *Riley 3162* (KE), *3163* (CLM); *ibid*, 3 Aug 2015, *Riley 3168* (OS), *3169* (KE), *3170* (CM), *3171* (UWO); *ibid*, 20 Aug 2015, *Riley 3172* (OS), *3173* (KE), *3174* (UWO), *3175* (CM); *ibid*, 3 May 2016, *Riley 3482* (OS), *3483* (KE), *3484* (CLM), *3485* (CM); *ibid*, 6 May 2016, *Riley 3486* (OS), *3487* (KE), *3488* (MU), *3489* (MICH); *ibid*, 24 Apr 2017, *Riley 3830* (OS), *3831* (KE); Paris Twp., rare, two mature, healthy, flowering individuals in narrow strip between State Route 5 & RR, Camp Ravenna Joint Military Training Center, 11 May 2018, *Riley 4113* (OS), *4114* (KE), *4115* (CLM), *4116* (OS), *4117* (KE), *4118* (CM).

As explained in our discussion of county-record deletions (Section II), it is now known that this uncommon hawthorn does not naturally extend further west than northeastern Ohio. Due to its extreme rarity, *Crataegus pennsylvanica* was added to the Ohio Rare Plant List as a State Endangered species in 2018 (ODNR 2018).

22) ***CRATAEGUS ×PERSIMILIS*** Sargent (Rosaceae) – plumleaf hawthorn. **Crawford Co.**: Auburn Twp., mesophytic woods adjacent to the Celeryville Reservoir, 10 Jul 1965, *Ferencak & Jarzen s.n.* (KE). **Portage Co.**: NW ¼ Charlestown Twp., one young tree near S edge of early successional woods, Camp Ravenna Joint Military Training Center, 11 Aug 2015, *Riley 3141* (KE), *3142* (UWO); *ibid*, 22 May 2017, *Riley 3815* (OS), *3816* (KE), *3817* (UWO). **Trumbull Co.**: Braceville Twp., shore of beaver pond, 10 Jun 1943, *Rood 1914* (KE).

Phipps (2014) stated that *Crataegus ×persimilis* is plausibly an intersectional hybrid between *Crataegus crus-galli* L. and *Crataegus succulenta* (Loudon) Rehder "in the broad sense." Morphologically, this hybrid more closely resembles *Crataegus crus-galli*. The stamens in the Portage County individual cited above averaged ten per flower with dark pink to purple anthers.

23) ***CRATAEGUS SUBORBICULATA*** Sargent (Rosaceae) – Caughuawaga hawthorn. **Portage Co.**: Edinburg Twp., single tree growing on upland mesic site on edge of young, successional woods, West Branch Wildlife Area, 1 Sep 2016, *Riley 3493* (UWO); *ibid*, 9 May 2017, *Riley 3844* (OS), *3845* (KE), *3846* (UWO); *ibid*, 13 Jun 2017, *Riley 3847* (OS), *3848* (KE), *3849* (UWO – two sheets); *ibid*, 17 Jun 2017, *Riley 3850* (UWO); *ibid*, 4 Aug 2019, *Riley 4282* (CLM), *4283* (CM), *4284* (MICH).

This shrub to small tree was reported from Ohio by Braun (1961) and Kartesz (2015) based on incorrectly identified and unrelated collections from five scattered counties including one from a somewhat ambiguous location in Ottawa County with no date or collector information given. See the entry in Section II for more details. Given its similarity to the common and widespread *Crataegus pruinosa* (Wendl.) K. Koch and its four recognized varieties (Phipps 2014), it is extremely important

to collect mature, fruiting specimens while noting diameter of mature pomes and number of stamens. Mature, non-deformed pomes examined later in the growing season will reveal whether or not they are pruinose – a relatively easy to discern distinction between *Crataegus pruinosa* and *Crataegus suborbiculata*. If collecting flowering material, the color of fresh anthers should also be included on the label. In the case of the Portage County, Ohio, population discovered in 2016, this species occurs in association with other members of series *Pruinosae*, including *Crataegus pruinosa* and *Crataegus macrosperma* Ashe.

24) ***CYCLOSPERMUM LEPTOPHYLLUM*** (Pers.) Sprague ex Britton & P. Wilson (Apiaceae) – marsh parsley. **Franklin Co.**: Ornamental grass planting array, SW corner of Recreation and Physical Activity Center, east side of Lincoln Tower Park, 150 m N of John Herrick Drive, Ohio State University, Columbus, 26 Jun 2014, *Klips s.n.* (OS).

Cyclospermum leptophyllum is a weedy annual native to South America, that has spread to both subtropical and temperate areas around the world (Ronse et al. 2010). USDA NRCS (2019) reported occurrences from every state in the continental US south of the 37th parallel as well as every state bordering the Atlantic seaboard from New York south to Florida. Prior to the Franklin County, Ohio discovery, the closest and only Midwestern occurrences of this species were from Champaign County, Illinois, where it was found growing as a weed within an ornamental planting and within turfgrass along a nearby roadside (Illinois Wildflowers 2019). Neither a one-time waif nor a long-term naturalizer, the species was collected once in an ornamental grass planting where it grew in association with *Senecio vulgaris* and *Sonchus* sp. According to Dr. Robert A. Klips (pers. comm.), this population persisted for a few years until the ornamental grass planting was replaced with sod.

25) ***DIOSPYROS VIRGINIANA*** L. var. ***PUBESCENS*** Nutt. (Ebenaceae) – common persimmon. **Mahoning Co.**: Jackson Twp., weed along RR tracks, NW of Jackson Center, 19 Jul 1960, *Cooperrider 7054* (KE). **Pickaway Co.**: Walnut Twp., section 30, three non-fruiting saplings, locally escaped from planted trees in nearby private orchard, Stages Pond State Nature Preserve, Ashville, 27 Aug 2017, *Riley 3870* (OS). **Trumbull Co.**: Braceville Twp., adventive from cultivated trees, 20 Jun 1954, *Rood 2821* (KE).

Variety *pubescens*, with villous or densely tomentose branchlets and leaves abaxially hairy, occurs just south of Ohio. The natural range of this variety spans from Florida west to Arkansas, north to Virginia, southern Illinois, and southern Iowa (Fernald 1950). All Ohio collections cited here are local escapes from cultivated trees selected for their fruit size and yield.

26) ***DISTICHLIS SPICATA*** (L.) Greene (Poaceae) – saltgrass. **Portage Co.**: N ½ Ravenna Twp., large, local, rhizomatous population growing in black, saline soil along N edge of SR 14, Ravenna, 27 Jun 2017, *Riley 3871* (OS), *3872* (KE), *3873* (CLM), *3874* (CM).

Vincent and Cusick (1998) cited a single collection from Lake County, collected 20 Sep 1991 by J.K. Bissell. Given the fact that the only other collection from Ohio occurred 26 years after the first, it would seem that this halophyte is not rapidly spreading despite the abundance of suitable habitat along salted highways and other disturbed areas.

27) ***DITTRICHIA GRAVEOLENS*** (L.) Greuter (Asteraceae) – stinkwort. **Portage Co.**: SE ¼ SE ¼ Streetsboro Corporation Limit, locally abundant, weedy population consisting of thousands of individuals growing in full sun on dry, gravelly, saline soil along NE edge/berm of SR 14, Streetsboro, 16 Sep 2018, *Riley 4139* (OS), *4140* (KE), *4141* (CLM), *4142* (CM); *ibid*, 18 Sep 2018, *Riley 4143* (OS), *4144* (KE), *4145* (BHO), *4146* (MU), *4147* (MICH).

Preston (2006) reported this species as being introduced in the US (California, Connecticut, New Jersey, New York), from southwestern Italy, India, South Africa, and Australia, where it occurs in disturbed fields, roadways, and estuarine borders. The highway along which the Ohio population was found was closed from 3 Oct 2016 to 23 Mar 2017 for bridge repair. This now very abundant species had not been observed or collected at this site before the closure, though it was later seen by Riley in similar disturbed roadside habitats elsewhere in Portage County in September 2019. Given this sudden and prolific occurrence, it comes as no surprise that Preston (2006) made reference to late 1940s collections from New York that described it as "abundant in areas where road construction was underway." Due in part to contaminated construction equipment, additional populations are likely to become established in similar open and disturbed areas throughout Ohio and beyond, as has already been the case in at least four other states, including California where it is spreading most rapidly and displaying the potential to become a noxious weed (Preston 2006).

28) ***ELEOCHARIS MACROSTACHYA*** Britton (Cyperaceae) – pale spikerush. **Fayette Co.**: Union Twp., extremely abundant in open wetland along either side of boardwalk trail, Shaw Wetland, Washington Court House, 30 May 2012, *Riley 2359* (OS); Union Twp., extremely abundant in dense, clonal colonies within marshy shallows around perimeter of Crooked Creek detention pond, Washington Court House, 15 Jun 2013, *Riley 2706* (OS), *2707* (MU), *2708* (MICH), *2709* (BHO), *2710* (CLM). **Pickaway Co.**: Perry Twp., locally common, moist mud of man-made marsh, Deer Creek Wildlife Area, 28 Sep 2007, *Gardner 5670 & McCormac* (MICH); Perry Twp., small, local population growing in seasonally wet depression beside gravel access at SW corner of field, Deer Creek Wildlife Area, 6 Jun 2012, *Riley 2360* (OS), *2361* (MICH); Perry Twp., locally scattered, dense, clonal populations occurring in seasonally wet depressions throughout a fallow field, Deer Creek Wildlife Area, 23 Jun 2013, *Riley 2711* (OS), *2712* (BHO), *2713* (MU), *2714* (CLM), *2715* (MICH).

This species was first discovered in Ohio in Sep 2007 by Gardner and McCormac at Deer Creek Wildlife Area in Pickaway County. A specimen from this site/collection was identified as *Eleocharis macrostachya* by Dr. A.A. Reznicek after co-author Riley had found it nearby in neighboring Fayette County in May 2012. In 2014, this species was determined to be native by the Ohio Rare Plants Advisory Committee. The basis for this determination was that these multiple occurrences were located within an area of the state well-known for many extant and extirpated western disjuncts and prairie wetland endemics.

29) ***ERAGROSTIS CURVULA*** (Schrad.) Knees (Poaceae) – weeping lovegrass. **Jackson Co.**: Jefferson Twp., section 14, local, 7 individuals in full sun on dry, sandy soil on E side of narrow, grassy trail, Jackson Lake State Park, Oak Hill, 8 Jun 2018, *Riley 4149* (OS). **Lawrence Co.**: Elizabeth Twp., section 31, locally common in powerline right-of-way, dry, sandy soils, Wayne National Forest, 8 Jun 2009, *Gardner 6252* (OS); Decatur Twp., section 26, ca. 30 locally scattered individuals/clumps on dry, sandy SW-facing slope along Tarkiln Bridal Trail, Dean State Forest, 1 Sep 2014, *Riley 2955-2956*

(OS); *ibid*, 24 Jun 2017, *Riley 3876* (OS), *3877* (BHO), *3878* (KE). **Portage Co.**: woodlot, men's dorm, Kent State University, 28 Jun 1955, *P.A. Bricker s.n.* (KE).

The provenance of the Portage County specimen is uncertain; it is unclear whether it was from cultivation or from a naturalized or escaped population.

30) ***EUONYMUS BUNGEANUS*** Maxim. (Celastraceae) – winterberry euonymus. **Licking Co.**: Alternative farm, NW corner of white pine plantation, The Dawes Arboretum, 6 Jun 2015, *Brandenburg & Messinger s.n.* (DAWES).

Like other species of its genus, *Euonymus bungeanus* has a propensity to spread, primarily via birds (Li et al. 2006). Native to northern China and hardy to zone 4 (Univ. of Connecticut 2018), this species is likely to spread in Ohio, first in and around areas where planted ornamentally and, in time, well beyond.

31) ***EUPATORIUM GODFREYANUM*** Cronq. (Asteraceae) – Godfrey's thoroughwort. **Hocking Co.**: Laurel Twp., on ledge of steep, rocky cliff in oak-pine forest, west cliff of Hood Hollow, Crane Hollow Preserve, 12 Aug 2011, *Moosbrugger 11-309* (BHO). **Jackson Co.**: Liberty Twp., old field near Oakland School, 3 Aug 1958, *Bartley 2402* (NY). **Lawrence Co.**: Washington Twp., dry, open, S-SW facing roadside slope within narrow powerline clearing on upland/hilltop site, 10 Aug 2013, *Riley 2720* (OS), *2721* (BHO); *ibid*, 25 Aug 2017, *Riley 3879* (OS), *3880* (KE). **Pike Co.**: Jackson Twp., growing in full sun on dry, upland, W-facing sandstone outcrop, 26 Aug 2017, *Riley 3881* (OS). **Scioto Co.**: Nile Twp., 70-80 flowering plants growing in patch in open powerline cut in dry, rocky, acidic soil over sandstone on SW facing slope, Shawnee State Forest, 10 Aug 2018, *Gibson 235* (OS).

Cronquist (1985) reported a collection from Jackson County, which is cited above. Perhaps best described in the casual sense as a "hairy *Eupatorium sessilifolium*," this species was long presumed to be a stable hybrid between *Eupatorium rotundifolium* L. and *Eupatorium sessilifolium* L. until elevated to the rank of species by Cronquist (1985). Its ancestral hybridity was ultimately later confirmed by Siripun & Schilling (2006a). Where it occurs throughout its range, populations are persistent and occur with or without both putative parents nearby. For comparative purposes, there is a voucher of a true, F_1 *Eupatorium rotundifolium* × *Eupatorium sessilifolium* hybrid at OS (*Riley 2379*), which is also cited herein as a new taxon in the Ohio flora. It should be noted that this F_1 cross morphologically resembles *Eupatorium godfreyanum*, which evolved from as a cross between these same two species (Siripun & Schilling 2006a).

32) ***EUPATORIUM PILOSUM*** Walt. (Asteraceae) – rough boneset. **Athens Co.**: York Twp., few local populations growing in wet, acidic, *Sphagnum* seeps and depressions on open mine-spoil site within large powerline clearing/right-of-way, Wayne National Forest, 17 Aug 2013, *Riley* 2722 (OS), *2723* (BHO), *2724* (CLM); *ibid*, 18 Aug 2013, *Riley 2725* (MU); *ibid*, 22 Aug 2015, *Riley 3216* (KE), *3217* (CM). **Gallia Co.**: Cheshire Twp., palustrine emergent depression, low pH acid impaired (strip mine) sandy clay substrate, 12 Jul 2010, *Walters 12842 & Kusnier* (CLM, MICH). **Hocking Co.**: Green Twp., small, locally scattered individuals occurring within acidic, marshy area along small drainage on edge of mature forest, Dorr Run APV Area, Wayne National Forest, 10 Aug 2014, *Riley 2962* (OS). **Lawrence Co.**: Hamilton Twp., section 7, small, local population of mostly sterile individuals

occurring on poorly drained, acidic, open, 0.50-acre mine-spoil site, Hanging Rock Recreation Area, Wayne National Forest, 26 Jul 2014, *Riley 2963* (OS); *ibid*, 1 Sep 2014, *Riley 2964* (OS); Hamilton Twp., section 1, uncommon, small population consisting of perhaps six to eight locally scattered individuals growing on dry to moist soil at/near SE end of successional opening within abandoned strip-mined area, Hanging Rock Recreation Area, Wayne National Forest, 1 Sep 2018, *Riley 4151* (OS).

The Ohio Rare Plants Advisory Committee determined in 2016 that it would be most appropriate to treat this species as native to the region, but adventive in Ohio. Although this species is believed to have established at each of the four known sites naturally, these sites are man-made spoil areas from un-reclaimed mining operations and coal-ash deposits. As such, the presence of this species in Ohio is unlikely to have pre-dated European settlement. Further substantiating this claim is the known distribution of *Eupatorium pilosum*, which does not include Ohio but does include the bordering states of Kentucky, Pennsylvania, and West Virginia (Siripun & Schilling 2006b).

The following three entries are all unnamed interspecific *Eupatorium* hybrids, which, in each case, were found growing in association with their respective putative parents.

33) ***EUPATORIUM PERFOLIATUM*** L. × ***EUPATORIUM ALTISSIMUM*** L. (Asteraceae) – hybrid thoroughwort. **Muskingum Co.**: Newton Twp., section 16, small, local population of several hybrid individuals growing in association with both parent species on E side of gravel road/access lane within abandoned strip-mine area, Avondale Wildlife Area, 31 Aug 2012, *Riley 2376* (OS).

34) ***EUPATORIUM SEROTINUM*** Michx. × ***EUPATORIUM SESSILIFOLIUM*** (Asteraceae) – hybrid thoroughwort. **Ross Co.**: Harrison Twp., section 23, 5-10 plants, maybe more, near horse trail along mid-slope, steep, brushy, cut over open oak woods, Boblett Hollow, Tar Hollow State Forest, 4 Aug 2012, *Minney s.n.* (OS). **Vinton Co.**: Vinton Twp., section 35, small, local population growing in association with both parental species in mature, dry, upland oak woods, Vinton Furnace Experimental Forest, 5 Aug 2012, *Riley 2377-2378* (OS).

35) ***EUPATORIUM SESSILIFOLIUM*** × ***EUPATORIUM ROTUNDIFOLIUM*** (Asteraceae) – hybrid thoroughwort. **Jackson Co.**: Liberty Twp., section 25, two local individuals growing among both parental species on open, ridgetop site within a recently clear-cut area, 5 Sep 2012, *Riley 2379* (OS).

36) ***EUPATORIUM*** ×***TRUNCATUM*** Muhl. ex Willd. (*Eupatorium serotinum* × *Eupatorium perfoliatum*) (Asteraceae) – truncate-leaved thoroughwort. **Gallia Co.**: Raccoon Twp., section 11, two individuals growing in association with both parental species in small opening on NW edge of young, low, wet woods, Tycoon Lake State Wildlife Area, 25 Aug 2017, *Riley 3886* (OS); Walnut Twp., section 19, one individual growing in association with both parent species within open, marshy, acidic wetland at entrance to Flagsprings Cemetery, 1 Sep 2018, *Riley 4152* (OS). **Hocking Co.**: Good Hope Twp., section 26, two plants growing at top of narrow, 25'-wide powerline clearing on NE-facing ridgetop, Rockbridge, 17 Sep 2011, *Riley 1997* (OS). **Jackson Co.**: Liberty Twp., section 25, one vigorous individual growing in presence of parental species within open, recent clear-cut, ridgetop site, 23 Aug 2014, *Riley 2968* (OS), *2969* (BHO). **Muskingum Co.**: Newton Twp., section 16, locally scattered hybrids growing along E & W sides of dirt road/access lane within abandoned strip-mine area,

Avondale Wildlife Area, 31 Aug 2012, *Riley 2374* (OS). **Portage Co.**: Windham Twp., two individuals growing in dry, open, weedy, gravelly area near concrete pad with both parental species nearby, Camp Ravenna Joint Military Training Center, 17 Sep 2013, *Riley 2729* (OS); *ibid*, 23 Sep 2013, *Riley 2730* (CLM). **Ross Co.**: Jefferson Twp., section 12, one robust individual growing with both parental species located near NE corner of recently clear-cut floodplain site, 5 Aug 2012, *Riley 2375*, *Boone, Minney, & Bens* (OS). **Trumbull Co.**: Braceville Twp., locally scattered, growing in association with both parental species within 150-foot wide clearing surrounded by mature, wet-somewhat poorly drained pin oak flatwoods, Camp Ravenna Joint Military Training Center, 2 Sep 2015, *Riley 3220* (OS).

This interspecific hybrid has been collected eight times in seven widely scattered Ohio counties since its discovery in 2011. Kartesz (2015) mapped its distribution in 18 states throughout the eastern US. While *Eupatorium perfoliatum* is extremely common and can most likely be found in all 88 Ohio counties, the other parent, *Eupatorium serotinum*, is less common but may become more widespread throughout the state in moist and dry open areas, where it is commonly found along railroads, thickets, disturbed yards, and roadsides (Michigan Flora Online 2019). Fisher (1988) reported collections of *Eupatorium serotinum* from only 15 counties, most located in the southern quarter of the state. Due to the broad distribution of *Eupatorium perfoliatum* and the spread of *Eupatorium serotinum* into parts of Ohio where it had not been seen until recently, additional hybrid populations are likely to occur.

37) ***HIPPOPHAE RHAMNOIDES*** L. (Elaeagnaceae) – sea-buckthorn, seaberry. **Ashtabula Co.**: Geneva Twp., small, local population of arborescent shrubs persisting and thriving in sandy-loam soil at old homesite on edge of wooded shoreline, Geneva State Park, 1 Jun 2014, *Riley 2974 & Beechey* (OS), *2975* (CLM).

Sea-buckthorn is known as an escape in Canada, in the provinces of Alberta, Ontario, Quebec, Saskatchewan, and Yukon (Brouillet et al. 2010+).

38) ***HOUSTONIA PUSILLA*** Schoepf (Rubiaceae) – tiny bluet. **Hamilton Co.**: along Miami-Whitewater Bike Trail, south of Baughman Rd., north of New Haven Rd., 3 May 2014, *Boone & Decker s.n.* (MU).

Houstonia pusilla is an annual native to the midwestern, southern, and southeastern US (including Indiana and Kentucky) with introduced populations reported from Arizona, Delaware, and New York (Kartesz 2015).

39) ***JUNCUS SUBCAUDATUS*** (Engelm.) Coville & Blake (Juncaceae) – whitetail (woodland) rush. **Fairfield Co.**: Madison Twp., section 13, locally abundant, thousands of plants growing in semi-shaded, marshy alder thicket at headwaters of Lake Ramona, Clear Creek Metro Park, 1 Aug 2012, *Riley 2436* (OS); *ibid*, 3 Aug 2012, *Riley 2437* (OS), *2438* (MICH); *ibid*, 22 Aug 2012, *Riley 2439* (CLM), *2440* (MICH). **Jackson Co.**: Liberty Twp., section 17, local population growing within shrubby thicket in marshy seep, 5 Aug 2012, *Riley 2441*, *Boone, Minney, & Bens* (OS).

Historical records for this species in Ohio are known from Hocking and Ross Counties (Braun 1967). At the time this species was rediscovered in 2012 by Riley (Fairfield County) and Minney (Jackson County), it was listed as presumed extirpated in Ohio (ODNR 2018), since it had not been

seen in at least 20 years. Both the Fairfield County and Jackson County populations represent new county records for this rush.

40) ***MAGNOLIA STELLATA*** (Siebold & Zucc.) Maxim. (Magnoliaceae) – star magnolia. **Portage Co.**: NW ¼ Streetsboro Twp., one escaped, non-fruiting individual growing on mesic, somewhat poorly drained site, S side of boardwalk trail within small canopy opening, Tinker Creek Area of Liberty Park, Streetsboro, 14 Sep 2014, *Riley 2992* (OS), *2993* (KE), *2994* (CLM).

Vincent and Cusick (1998) cited two collections of star magnolia from Bishop Woods on the campus of Miami University in Butler County, collected in 1995 and 1997.

41) ***MORUS ALBA*** L. × ***MORUS RUBRA*** L. (Moraceae) – hybrid mulberry. **Brown Co.**: Pike Twp., mature, non-planted tree located along S edge of small woodlot & along wooded fence line on NE side of Sovereign Grace Baptist Church, White Oak, 18 Aug 2005, *Riley 309* (OS); *ibid*, 1 Jul 2006, *Riley 458* (OS). **Cuyahoga Co.**: tree, 6 m tall, in heavy forest cover, Hemlock Grove Picnic Area, Bedford Reservation – Cleveland Metroparks, 21 Aug 1985, *Goldsworth 59* (KE). **Hocking Co.**: Good Hope Twp., section 28, one triple-stem tree growing on E edge of upland, mesic woods & on W edge of hayfield, Rockbridge, 17 Sep 2016, *Riley 3538* (OS), *3539* (BHO), *3540* (KE). **Pickaway Co.**: Walnut Twp., section 30, mature, healthy tree growing on rich, open, mesic site within successional meadow, Stages Pond State Nature Preserve, Ashville, 27 Aug 2017, *Riley 3909* (OS), *3910* (MU). **Portage Co.**: Charlestown Twp., one mature tree growing in rich, mesic woods near N side of old homesite, Camp Ravenna Joint Military Training Center, 4 Sep 2015, *Riley 3252* (OS), *3253* (KE). **Summit Co.**: Boston Twp., moist alluvial woods, ½ mile N of Peninsula, 27 Jul 1960, *Cooperrider 7525 & Herrick* (KE). **Vinton Co.**: Vinton Twp., section 20, one healthy, naturally-occurring, double-stemmed tree growing on W edge of mesic woods in association with *Acer rubrum* and *Prunus serotina*, Radcliff, 5 Oct 2019, *Riley 4285* (OS), *4286* (KE), *4287* (BHO), *4288* (MU).

Unlike the native *Morus rubra*, *Morus alba* is a non-native species introduced to eastern North America in the early 17th century (Burgess & Husband 2006). As stated by Burgess et al. (2005), this hybrid and its later-generation backcrosses are becoming common wherever one parental species is relatively infrequent in relation to the other. In all probability, this hybrid is much more common throughout Ohio than these few collections indicate. Extreme caution must be applied when making *Morus* collections, as even typical specimens of *Morus rubra* and *Morus alba* can be difficult to distinguish, especially when immature. For added certainty, all collections cited above were taken from large, mature, fruiting individuals, which clearly exhibited fully developed characteristics of both parental species, including growth habit and bark pattern.

42) ***PHOTINIA VILLOSA*** (Thunb.) DC. (Rosaceae) – Oriental photinia. **Licking Co.**: Shrub, ca. 1 m tall, growing spontaneously on wood edge, east side, The Dawes Arboretum, 6 Oct 2015, *Brandenburg, Messinger, & Byrd s.n.* (DAWES).

Nesom (2014) included Ohio in the North American distribution of this Asian species, while Kartesz (2015) did not. The source of the record cited by Nesom is unknown.

43) ***POLYGONUM RAMOSISSIMUM*** Michx. subsp. ***PROLIFICUM*** (Small) Costea & Tardif (Polygonaceae) – bushy knotweed. **Wood Co.**: US Rt. 6 west of I-75, near Rudolph Rd., 23 Aug 2015, *Boone s.n.* (MU).

Polygonum ramosissimum subsp. *prolificum* is a widely distributed annual occurring in wet, saline soil throughout the continental United States and the southernmost six Canadian provinces (Costea et al. 2005). Costea et al. (2005) reported that while subsp. *prolificum* occurs in Ohio's bordering states of Kentucky and West Virginia, it has not been found in Indiana, Michigan, or Pennsylvania.

44) ***PRENANTHES ALTISSIMA*** L. var. ***HISPIDULA*** Fern. (Asteraceae) – tall rattlesnakeroot. **Pickaway Co.**: Washington Twp., section 10, local, clonal colony growing on top of bluff above tributary along Perimeter Loop Trail, A.W. Marion State Park, 10 Aug 2013, *Riley 2783* (OS); *ibid*, 17 Aug 2013, *Riley 2784* (OS), *2785* (BHO).

Although the typical variety is common and widespread in open deciduous hardwood or mixed woods, slopes, bluffs, and roadsides from the Atlantic coast west to Oklahoma and Texas, specimens of this variety, characterized by its densely hairy stems and pale yellow pappi, have been mostly found in New York, New England, and eastern Canada (Bogler 2006).

45) ***PRUNUS ANGUSTIFOLIA*** Marsh. (Rosaceae) – Chickasaw plum. **Clermont Co.**: E-SE Batavia Twp., small, fruiting population along bridle trail, East Fork State Park, 15 Aug 2006, *Riley 473 & Weber* (OS). **Gallia Co.**: Walnut Twp., section 32, large naturalized population located on open ridgetop (possibly an old homesite), Wayne National Forest, 4 Aug 2007, *Riley 702* (OS), *703* (MU); *ibid*, 26 Jul 2014, *Riley 3012* (BHO), *3013* (KE). **Wood Co.**: Plain Twp., section 36, small, escaped, mature, clonal population located along W edge of Slippery Elm Bike Trail, Bowling Green, 10 Jul 2007, *Riley 704-705* (OS).

In Ohio, *Prunus angustifolia* occurs either in naturalized populations or as local escapes. This southern species, which is reported to be infrequent across Kentucky (Jones 2005), is not considered to have been native to Ohio prior to European settlement. Cooperrider et al. (2001) deleted Chickasaw plum from the Ohio flora, as they were unable to locate any documenting specimens.

46) ***PRUNUS AMERICANA*** Marsh. × ***PRUNUS HORTULANA*** L.H. Bailey (Rosaceae) – hybrid plum. **Marion Co.**: Big Island Twp., section 33, one naturally occurring clonal population growing in open, early successional managed prairie ecosystem, Big Island Wildlife Area, 2 Jul 2008, *Riley 980-982* (OS); *ibid*, 20 Aug 2010, *Riley 1667-1668* (OS); *ibid*, 26 Apr 2011, *Riley 2861* (OS – four sheets); *ibid*, 29 Apr 2011, *Riley 2862* (OS – two sheets); *ibid*, 9 Aug 2011, *Riley 2863* (OS – eight sheets). **Warren Co.**: Eastern Wayne Twp., mature, clonal thicket consisting of seven mature trees observed along S edge of tall-grass prairie restoration, Caesar Creek Wildlife Area, 10 Sep 2005, *Riley 306* (OS); *ibid*, 28 Aug 2010, *Riley 1669-1670* (OS); *ibid*, 22 Apr 2011, *Riley 2864* (OS – two sheets). **Wood Co.**: Plain Twp., section 36, large, clonal thicket in open area along wire fencerow, Bowling Green, 24 Apr 2007, *Riley 725* (OS), *726* (MU); *ibid*, 10 Jul 2007, *Riley 727* (BGSU), *728* (MU); *ibid*, 15 Aug 2007, *Riley 729* (OS), *730* (MU); Liberty Twp., section 12, small clonal fruiting population located along W edge of Slippery Elm Bike Trail, Portage, 19 Jul 2007, *Riley 733-734* (OS), *735-736* (MU); *ibid*, 10

Aug 2007, *Riley 737* (BGSU); *ibid*, 29 Apr 2008, *Riley 993* (OS). Montgomery Twp., section 12, one young clonal population of three individuals located along E side of parking lot, Bradner Preserve, Bradner, 25 Apr 2008, *Riley 992* (OS); *ibid*, 2 May 2008, *Riley 994* (OS); *ibid*, 11 Jun 2008, *Riley 996* (OS); *ibid*, 2 Sep 2011, *Riley 2865* (OS).

This naturally occurring hybrid is not uncommon in western and west-central Ohio where its parental species are sympatric. Both species are commonly found throughout the original prairie region of Ohio, as these collections suggest. It should be noted that there is a sterile specimen from Anderson Twp., Hamilton County at OS (*E.M. Herrick s.n.*, accession 59575) collected on 1 Jul 1957, which is labeled as *Prunus americana*, although it bears many characteristics of this hybrid, including scattered gland-tipped teeth along the leaf margin. Because this is only a sterile voucher with no corresponding flowering specimen to confirm its identity, it falls short of being accepted herein as this hybrid.

47) ***PRUNUS SUBHIRTELLA*** Miq. (Rosaceae) – Higan cherry. **Butler Co.**: Fairfield Twp., woods along heavily disturbed stream corridor, Jayfield Dr., Hamilton, 17 Sep 2018, *Vincent & Saupé 17742* (MU, NY). **Pickaway Co.**: Walnut Twp., section 23, three locally escaped seedlings from parent tree across road growing in needle mulch directly under bald-cypress in residential yard, Ashville, 2 Sep 2013, *Riley 2802* (OS), *2803* (MU). **Ross Co.**: Harrison Twp., section 22, one escaped, rather pendulous tree growing in canopy opening on upland, ridgetop site within mature oak-hickory forest, Tar Hollow State Forest, 26 Aug 2017, *Riley 3931* (OS), *3932* (BHO). **Union Co.**: southeast Jerome Twp., locally escaped sapling originating from weeping cultivar planted in adjacent backyard, growing under *Pinus sylvestris* in far backyard, Plain City, 27 Jul 2017, *Riley 3933* (OS), *3934* (KE), *3935* (MU).

This species has been previously reported for Ohio: Vincent and Cusick (1998) cited a Brown County collection, and Wilder and McCombs (2002) cited a specimen from Cuyahoga County. This widely planted ornamental, especially its weeping cultivar, is becoming more common in residential landscapes, and, thus, will likely become increasingly common as an escape, as these four additional county records suggest.

48) ***PYRUS PYRIFOLIA*** (Burm. f.) Nakai (Rosaceae) – Chinese pear. **Gallia Co.**: Ohio Twp., section 2, one healthy, escaped tree growing on S-facing slope in young, dry, semi-open woods, Crown City State Wildlife Area, 5 Jul 2019, *Riley 4289* (OS), *4290* (MU). **Portage Co.**: Charlestown Twp., a single, naturalized, fruiting tree growing on edge of shrubby, successional field, Camp Ravenna Joint Military Training Center, 24 Oct 2013, *Riley 2806* (OS), *2807* (MU); *ibid*, 6 May 2014, *Riley 3030* (OS), *3031* (MU).

Pyrus pyrifolia is native throughout China, Laos, and Vietnam, and, although not often seen as an escape from cultivation, previous collections have been made from Illinois, Virginia, and West Virginia (Catling & Mitrow 2014). This species is widely available in the nursery industry due its delectable fruits which are neither similar in taste nor shape to *Pyrus communis* L. The Ohio collection cited here was made from a fruiting, local escape located not far from an old homesite.

49) ***QUERCUS COCCINEA*** Münchh. var. ***TUBERCULATA*** Sarg. (Fagaceae) – scarlet oak. **Coshocton Co.**: SW ¼ Tiverton Twp., mature, canopy tree growing on flat, dry-xeric ridgetop woods, Tiverton Center, 19 Jul 2011, *Riley 2103* (OS), *2104* (BHO). **Fairfield Co.**: Hocking Twp., section 7,

one mature tree growing on upper, S-SE-facing slope at SE corner of church property, Mt. Zion UM Church, Lancaster, 2 Jul 2012, *Riley 2516* (OS). **Scioto Co.**: Central Union Twp., one mature tree located in front yard near SW corner of house, Lombardsville, 2 Oct 2003, *Riley 572.01* (OS).

Braun (1961) reported that var. *tuberculata*, recognized by the thickened tuberculate scales of the acorn cup, occurs with the typical form in Pike and Scioto Counties. Such is the case for the three naturally occurring individuals cited above.

50) ***QUERCUS ×FERNOWII*** Trelease (*Quercus alba* L. × *Q. stellata* Wangenh.) (Fagaceae) – Fernow's oak. **Adams Co.**: SW ¼ Oliver Twp., one young, non-fruiting, double-stemmed tree located on S edge of woods in dry, open, blackjack-post oak opening, Johnson's Ridge State Nature Preserve, 2 Jul 2005, *Riley 577.01-577.02* (OS). **Champaign Co.**: Urbana Twp., section 17, one mature tree located within Section 45 of the Oakdale Cemetery, Urbana, 1 Dec 2002, *Riley 577.03* (OS); *ibid*, 6 Jun 2005, *Riley 577.04-577.05* (OS); *ibid*, 7 Oct 2005, *Riley 577.06 & Weber* (OS). **Madison Co.**: Jefferson Twp., one mature individual located on S side of tennis courts at Westwood Memorial Park, West Jefferson, 13 Jun 2003, *Riley 577.07* (OS). **Scioto Co.**: Washington Twp., one large tree growing at top of hill at SW corner of house, West Portsmouth, 26 Nov 2004, *Riley 577.08* (OS).

Braun (1961) cited Scioto County in her statewide distribution for this nothospecies based on a 1951 specimen consisting of two sheets she collected from a tree at Copperhead Fire Tower within Shawnee State Forest. In 1961, this specimen was in the private collection of E.L. Braun. Unable to locate the specimen four decades later, Cooperrider et al. (2001) deleted *Quercus ×fernowii* from the Ohio flora citing "no specimen."

51) ***RANUNCULUS SARDOUS*** Crantz (Ranunculaceae) – hairy buttercup. **Adams Co.**: Meigs Twp., along St. Rt. 73 between Portsmouth and Jaybird Rd., pasture, 12 Jun 2008, *Becus 61208* (OS). **Butler Co.**: Weedy in lawn, university campus, Oxford, 5 Apr 2016, *Vincent 17492* (MU); *ibid*, 29 Apr 2016, *Vincent 17495* (MU). **Clermont Co.**: near Perrintown, horse pasture, 16 May 2008, *Becus 51608* (OS). **Hancock Co.**: Findlay, racetrack at county fairgrounds, East Sandusky St., weedy ground, 12 Jun 1996, *Cusick 33128* (OS). **Huron Co.**: Huron County Fairgrounds, west of Ridge Rd. south of Norwalk, moist, sunny ground, 8 May 1998, *Cusick 34305* (OS). **Licking Co.**: Hartford Twp., Hartford Fairgrounds, east of Fairgrounds Rd. grassy field, 9 Jun 1997, *Cusick 33852* (OS). **Lorain Co.**: Lorain County Fairgrounds, along Racetrack St., Rt. 18, Wellington, 2 Jun 1999, *Cusick 34992* (OS). **Madison Co.**: Madison County Fairgrounds, St. Rt. 38 North of London, weedy ground, 1 Oct 1996, *Cusick 33494* (OS). **Medina Co.**: Homerville, junction of US Rt. 224 and St. Rt. 301, weedy roadside, 2 Jun 1999, *Cusick 34989* (KE, OS). **Meigs Co.**: Meigs County Fairgrounds, northeast of junction of US Rt. 33 and St. Rt. 124, moist ground, 23 May 1998, *Cusick 34382* (OS). **Mercer Co.**: Mercer County Fairgrounds, Market St. west of Celina, wet ditch, 1 Jun 1998, *Cusick 34516* (KE, OS). **Noble Co.**: Olive Twp., County Fairgrounds, Fairground Rd., grassy fencerow, 5 Jun 1997, *Cusick 33835* (OS). **Ottawa Co.**: Limestone, Southwest of junction of Co. Rts. 62 and 75, weedy depression, 18 Jun 1996, *Cusick 33150* (OS). **Pickaway Co.**: Pickaway County Fairgrounds, center of racetrack, US Rt. 22, east edge of Circle, 15 May 2001, *Cusick 35867* (OS); extreme E Deer Creek Twp., horse pasture, 26785 Rector Rd. (T-106), 0.30 mi. N-NW of Hunsicker Rd. (T-108) & 1.80 mi. S of SR 138, 19 May 2012, *Riley 2524* (OS). **Pike Co.**: E Newton Twp., horse pasture and in adjacent wet ditch, Long Fork Rd. (CR 26), W-NW of SR 104, 19 May 2012, *Riley 2525* (CLM). **Portage Co.**: Randolph, animal barns

at county fairgrounds, St. Rt. 44, 13 Jun 2000, *Cusick 35497* (OS). **Summit Co.**: few plants in muddy puddle along oil well road S of Highland Rd. W of RR tracks, Brandywine Creek (SR 8) North Option, 11 Jun 2013, *Stover s.n.* (KE). **Trumbull Co.**: Mesopotamia Twp., Girdle Rd. south of Parks West Rd., horse pasture, 13 Jun 2000, *Cusick 35499* (OS). **Vinton Co.**: Elk Twp., about animal barns, 4-H Fairground, St. Rt. 93, 17 May 2000, *Cusick 35429* (OS). **Wayne Co.**: Marshallville, village park, South of Fulton Rd., weedy ground, 20 May 1994, *Cusick 31650* (OS). Baughman Twp., backyard at intersection of TR 221 and CR 32, Tope's Peat and Limestone, 24 May 1977, *Andreas 894* (KE).

Ranunculus sardous, a European species, is widely established in the southeastern United States and further north along the east coast, as well as in sites in northeastern California and Oregon (Whittemore 1997). Wilder and McCombs (2002) made the first mention of this introduced species in Ohio, citing a specimen collected in eastern Cuyahoga County.

52) ***RUBUS ABLATUS*** L.H. Bailey (Rosaceae) – plains blackberry. **Butler Co.**: Bishop Woods, east of Upham Hall, Miami University campus, Oxford, 2 Jun 1997, *Shockey 22* (MU – two sheets). **Coshocton Co.**: Lafayette Twp., fencerow at Fairfield Cemetery, 5 Jun 2001, *Cusick 35948* (ISC, OS – two sheets). **Darke Co.**: Greenville Twp., section 34, Shawnee Prairie Preserve, Ohio Route 502, just west of Greenville, 6 Jun 2003, *Vincent 11016 et al.* (MU). **Hamilton Co.**: McFarlan Woods, Mount Airy Forest Park, Cincinnati, 7 Sep 1935, *Hutchinson s.n.* (BH). **Lawrence Co.**: Hamilton Twp., uncommon, edge of woods at cemetery, 21 Jun 2001, *Cusick 35966* (ISC, OS – two sheets). **Muskingum Co.**: Cass Twp., frequent, RR embankment, Adams Mills, 5 Jun 2001, *Cusick 35952* (ISC, OS – two sheets). **Ottawa Co.**: South Bass Island, near the lighthouse, Put-in-Bay, 27 Jun 1947, *Gordon 47-8* (BH – two sheets); 31 Jul 1948, *Grover & Verduin 48-4* (BH). **Pickaway Co.**: Walnut Twp., SE ¼ section 30, very common species throughout open areas at Stages Pond State Nature Preserve, Ashville, 19 Jul 2005, *Riley 170* (OS); *ibid*, 30 Jul 2018, *Riley 4190* (OS – three sheets). **Tuscarawas Co.**: 3 Jul 1948, *Davis & Davis 8777* (BH).

We suspect that this species may be much more abundant in Ohio than these records indicate, as it occurs throughout the Midwest and is especially common in Iowa and Missouri from where it was described (Widrlechner 2013). Unfortunately, many vouchers of Ohio's representatives of *Rubus* section *Arguti* (Rydb.) L.H. Bailey are too fragmentary to identify to species.

53) ***RUBUS ABORIGINUM*** Rydb. (Roscaeae) – garden dewberry. **Athens Co.**: Jul 1939, *Abbott 1157* (MU). **Auglaize Co.**: St. Marys, 21 May 1898, *Wetzstein 5434* (MU). **Hocking Co.**: Benton Twp., section 9, edge of old road through young oak woods on ridgetop, Camp Oty-Okwa, 17 May 2000, *Cusick 35436* (OS); Good Hope Twp., section 28, locally scattered, not particularly abundant low-arching species with tip rooting primocanes and floricanes with large ascendate infructescences lacking stipitate glands on pedicels, population growing on dry, S-facing upper slope on edge of mature upland scarlet-chestnut oak woods, 19 Jun 2015, *Riley 3291* (OS – two sheets). **Jefferson Co.**: Salem Twp., floor of open ash woods, floricanes low arching, rooting at tips, Sanders farm, ¼ mi. NE of Annapolis, 29 May 1964, *Herrick s.n.* (OS). **Lucas Co.**: palustrine wet meadow with few shrubs, Kitty Todd Preserve, Mancy Tract (TNC), 1 Jun 1995, *Walters 1995:041* (CLM). **Mahoning Co.**: Poland Twp., occasional in openings on reclaimed soils, Carbon Limestone Sanitary Landfill Facility ca. 3.7 km SE of Poland Center, 26 May 1998, *Isaac 10601* (YUO – two sheets). **Ottawa Co.**: Camp Perry, wetland area in NW corner of site, 26 May 2005, *Godec CPO79* (MU). **Portage Co.**: SE ¼ Freedom Twp.,

local population consisting of low-arching, non-glandular canes with ascendate pedicels sprawling over pavement on E edge of D-Block Lane 3, Camp Ravenna Joint Military Training Center, 11 Aug 2017, *Riley 3943* (ISC – three sheets); *ibid*, 6 Jul 2018, *Riley 4195* (OS – four sheets). **Scioto Co.**: Madison Twp., NW ¼ Section 11, local population growing in full sun on dry-xeric, open roadside embankment, 6 Jul 2013, *Riley 2832* (OS – two sheets).

This species was the source of a number of popular dewberry cultivars in the late 1800s and early 1900s [as discussed under the synonym, *Rubus almus* L.H. Bailey, by Bailey (1943)]. However, in Ohio, we have not observed examples suggesting the persistence of old fruit cultivars; instead, the habitats in which this dewberry occurs are diverse and the plants more typical of unselected forms. We suspect that this species likely much more common than these few records indicate.

54) ***RUBUS ALUMNUS*** L.H. Bailey [syn. ***RUBUS COREI*** L.H. Bailey] (Rosaceae) – oldfield blackberry. **Darke Co.**: Jackson Twp., section 24, Coppess Nature Sanctuary, 16 Jul 2011, *Vincent 1946 & Cusick* (MU). **Harrison Co.**: 28 Jun 1900, *Kellerman s.n.* (OS). **Lorain Co.**: 18 Jun 1963, *Fuller & Fuller F-63-1* (MIL). **Ottawa Co.**: 20 Jul 1947, *Gordon 47-11* (BH); South Bass Island, 25 Jul 1947, *Gordon 47-16* (BH); Kelleys Island, 26 Jul 1947, *Gordon 47-5* (BH); Put-in-Bay, 29 Jul 1947, *Gordon 47-19* (BH); 31 Jul 1948, *Grover & Verduin* 48-1 (BH); 31 Jul 1948, *Grover & Verduin* 48-3 (BH). **Vinton Co.**: Vinton Twp., section 36, locally common, thickets at edge of woods, Vinton Furnace Experimental Forest, 17 May 2006, *Gardner 5194* (ISC).

The specimens noted above from Lorain and Ottawa Counties were the basis for Widrlechner (1998) mapping those two as the only Ohio counties in which this species had been collected at the time of that publication. The Lorain County collection of 29 Jul 1947 serves as the type for *Rubus corei* L.H. Bailey (Core 1948).

55) ***RUBUS ARGUTUS*** Link (Rosaceae) – sawtooth blackberry, southern blackberry. **Gallia Co.**: Ohio Twp., section 2, locally common, upright, non-glandular canes growing on seasonally wet – predominately dry, acidic, sandy clay soil within successional, mine-spoil area, Crown City State Wildlife Area, 28 Jul 2018, *Riley 4198* (OS – five sheets), *4199* (ISC – four sheets).

Rubus argutus is an extremely common species to the south of Ohio; in many parts of the southeastern US, it is perhaps the most common species of *Rubus*, but evidently has not often made its way as far north as Ohio. See entry in Section II for details concerning Ohio counties from which misidentified specimens were previously attributed.

56) ***RUBUS BEAMANII*** Widrlechner & Riley [*Rubus vagus* L.H. Bailey (*nom. illeg.*)] (Rosaceae) – Beaman's dewberry. **Portage Co.**: Paris Twp., rare, locally scattered, low-arching, tip-rooting glandular dewberry growing on hummocks and small rises within mature, densely shaded, high-quality swamp woods, Camp Ravenna Joint Military Training Center, 29 Jun 2017, *Riley 3944* (OS), *3945* (KE); Ravenna Twp., rare, one robust individual growing on rich, loam, mesic, open site, Shaw Woods Working Lands Park, Ravenna, 8 Jul 2017, *Riley 3946* (OS – two sheets); Shalersville Twp., rare, local, non-vigorous, low-arching, tip-rooting population growing in dense shade on S edge of rich, mature, mesic woods & on N side of drainage channel within open wetland, Morgan Preserve, 13 Aug 2017, *Riley 3947* (OS – two sheets), *3948* (KE – two sheets), *3949* (ISC – two sheets); SE ¼ Shalersville

Twp., uncommon; very local, low-arching, tip-rooting, glandular population on rich site within small (mostly shaded) canopy opening within mature, mesic woods, Morgan Preserve, Shalersville, 18 Jul 2018, *Riley 4202* (KE – three sheets). **Trumbull Co.**: Braceville Twp., rare, rather large, local fruiting population with low arching, tip-rooting canes growing on slightly elevated and acidic, loam, soil on W edge of mature pin oak flatwoods, Camp Ravenna Joint Military Training Center, 24 Jul 2017, *Riley 3950* (KE – four sheets), *3951* (MU – two sheets), *3952* (MICH – two sheets), *3953* (CM – two sheets), *3954* (CLM – two sheets); SW ¼ Green Twp., small, very local, non-robust and non-tip-rooting population subjected to filtered sunlight within understory of mature, swamp/flatwoods, Mosquito Creek State Wildlife Refuge, 1 Jul 2018, *Riley 4203* (ISC – three sheets); S ½ Bazetta Twp., uncommon; small, local, population growing on loam, moist-mesic site on edge of vernal pool within understory of densely shaded, mature swamp forest/flatwoods, Elm Road Public Hunting Area, Cortland, 15 Jul 2018, *Riley 4204* (KE – two sheets).

According to Widrlechner and Riley (2017), this potentially globally rare dewberry from section *Procumbentes* (Rydb.) L.H. Bailey (=*Flagellares* (L.H. Bailey) L.H. Bailey) was only extant in Ohio, with historical records from Kalamazoo County, Michigan. A recent review of all specimens of Michigan *Rubus* at MICH turned up records from three additional Michigan counties, including Benzie, Crawford, and Oscoda – the most recent having been collected in 1959. The Ohio vouchers referenced here do not include those which were previously cited in Widrlechner & Riley (2017). Beaman's dewberry was accepted in 2018 as native to the Ohio flora by the Ohio Rare Plants Advisory Committee, which placed it on the Ohio Rare Plant List as an "Added" species with possible state legal status pending further review and additional searching. This matter will be discussed when the committee reconvenes in 2020.

57) ***RUBUS CANADENSIS*** L. (Rosaceae) – Canadian blackberry, smooth blackberry. **Cuyahoga Co.**: local in semi-shaded edge habitat along trail through rocky gorge with hemlock-hardwood forest, South Chagrin Reservation – Cleveland Metroparks, 23 Jul 2019, *Reinier 1817* (KE – five sheets); *ibid*, 24 Jul 2019, *Reinier 1818* (KE – three sheets); local in seasonally wet woods, North Chagrin Reservation – Cleveland Metroparks, 29 Jul 2019, *Reinier 1822* (ISC – two sheets, KE – two sheets); local on steep ravine slope under beech-birch-maple-oak forest, South Chagrin Reservation – Cleveland Metroparks, 29 Aug 2019, *Reinier 1844* (KE – two sheets). **Lake Co.**: locally abundant at margin of a depression in wet woods, North Chagrin Reservation – Cleveland Metroparks, 12 Aug 2019, *Reinier 1832* (ISC – two sheets, KE – two sheets).

In late July through August 2019, John E. Reinier of the Cleveland Metroparks made several collections from native populations of *Rubus canadensis* located on Metropark property in Cuyahoga and Lake Counties. These vouchers were later verified as such by co-author Mark Widrlechner in October 2019, resulting in the first positively identified specimens of *Rubus canadensis* from Ohio.

Previous sources which had included this taxon as native to the Ohio flora did so based on incorrectly identified specimens housed at CLM and CM. See entry in Section II for additional information regarding those collections.

58) ***RUBUS CELER*** L.H. Bailey (Rosaceae) – swift dewberry. **Ashtabula Co.**: tip-rooting, scattered, brushy field, S of South Ridge Rd., city of Conneaut, 22 Jul 1994, *Cusick 31877* (OS).

Champaign Co.: 5 Jul 1950, *Davis & Davis 9074* (BH). **Portage Co.**: NW ¼ Paris Twp., small, local population growing on edge of mesic woods, Camp Ravenna Joint Military Training Center, 10 Aug 2017, *Riley 3987* (OS – two sheets), *3988* (ISC – two sheets). **Scioto Co.**: SW ¼ Union Twp., uncommon, located along S-SW edge of logging road on dry, open site, Shawnee State Forest, 22 Jun 2018, *Riley 4240* (ISC – six sheets).

In Widrlechner (1998), only Champaign County in Ohio was mapped for this dewberry, which resembles *Rubus flagellaris* Willd. except for the shape of its unshouldered primocane central leaflets and a few other minor characters. Widrlechner verified the Ashtabula County specimen as such in 2000.

59) ***RUBUS CENTRALIS*** L.H. Bailey (Rosaceae) – heartleaf dewberry. **Adams Co.**: dry oak woods, along the edge of woods near Johnson Ridge, 9 Jul 2015, *Boone s.n.* (ISC, MU).

This dewberry resembles the more common *Rubus invisus* (L.H. Bailey) Britton, which occurs in the same habitats throughout southern and southeastern Ohio, but differs from it by having consistently 1-flowered inflorescences and primocanes with distinctly cordate terminal leaflets which are wide-ovate (Widrlechner & Riley 2017). *Rubus centralis* has been reported from ten counties in southern Indiana (Kartesz 2015).

60) ***RUBUS CURTIPES*** L.H. Bailey (Rosaceae) – shortstalk dewberry. **Gallia Co.**: Walnut Twp., section 32, locally common, low arching species growing on dry ridgetop site in association with young, successional *Pinus virginiana*, Wayne National Forest, 26 Jul 2014, *Riley 3044* (OS – two sheets); *ibid*, 25 Aug 2017, *Riley 3955* (ISC – two sheets). **Hocking Co.**: Good Hope Twp., section 21, common, non-glandular bramble with low-arching, tip-rooting canes growing on dry, acidic, rather nutrient-poor soil within open, underground, gas-line clearing on or near hilltop site, Rockbridge, 24 Jun 2018, *Riley 4205* (OS). **Jackson Co.**: Liberty Twp., section 12, common, low-arching, tip-rooting, non-glandular species growing on dry ground in understory and on edge of young *Pinus virginiana* stand at base of S-facing sandstone wall where plants receive full-near full sunlight, Jackson, 8 Jun 2018, *Riley 4206* (OS – two sheets), *4207* (ISC – two sheets). **Lawrence Co.**: Washington Twp., section 12, local population with low arching primocanes & racemiform inflorescence with very short pedicels, growing in full sun on dry, shallow, rocky, sandy soil near small sandstone outcrop within narrow roadside powerline clearing, 10 Aug 2013, *Riley 2811* (OS – four sheets); *ibid*, 24 Jun 2017, *Riley 3956* (OS – two sheets), *3957* (ISC – two sheets). **Lorain Co.**: NE Amherst Twp., on old railroad embankment, 17 May 1970, *Jones 70-5-17-255* (OS). **Lucas Co.**: 9 Aug 1924, *Mosley s.n.* (OS). **Ross Co.**: Liberty Twp., section 11, local population on dry, open, rocky, acidic-clay soil at base of state champion *Pinus rigida*, Peecher Cemetery, Londonderry, 8 Jun 2018, *Riley 4208* (OS – two sheets), *4209* (ISC – three sheets). **Vinton Co.**: Harrison Twp., section 27, local population growing on dry, open, S & W-facing hillside along logging road within a dry, open, 2011 clear-cut site, 28 Jul 2013, *Riley 2826* (OS – three sheets). **Wayne Co.**: 5 Jul 1957, *Davis & Davis 11865* (CM).

Widrlechner (1998) did not map any Ohio counties as having a confirmed specimen of this glandless dewberry, despite the fact that it is widely distributed from Iowa and Minnesota, east to New Jersey and south to Tennessee. *Rubus curtipes* is likely to be fairly common throughout Ohio and should be sought in dry, open, somewhat disturbed habitats and successional fields.

61) ***RUBUS DEAMII*** L.H. Bailey (Rosaceae) – Deam's dewberry. **Lake Co.**: 3 Jun 1948, *Fuller F-48-1* (MIL). **Scioto Co.**: Green Twp., uncommon, local, healthy population (occasionally sprayed) with low-arching, tip-rooting, glandular-ascendate pedicels growing on disturbed, open site within ca. 375 square-foot area under overhead powerlines, Franklin Furnace, 9 Jun 2018, *Riley 4210* (OS – four sheets), *4211* (ISC – three sheets). **Vinton Co.**: Vinton Twp., section 30, oak-hickory forest, Vinton Furnace Experimental Forest, 10 May 1969, *Silberhorn 3341* (KE).

This species has been found to be scattered throughout the state, not common at any one location. In Ohio, *Rubus deamii* occurs on a variety of habitats, including oak-hickory forests, edges of successional woods, and in an open, successional meadow on rich, silt-loam soil. Kartesz (2015) presented a distribution map, which includes five Ohio counties (Erie, Hamilton, Knox, Montgomery, and Ottawa), based on Braun (1961) and Stuckey and Duncan (2010). We have not been able to verify the specimens upon which those records were based.

62) ***RUBUS DENSISSIMUS*** H.A. Davis & T. Davis (Rosaceae) – Morgantown blackberry. **Lucas Co.**: N of Monclova Rd. and E of the Girdham Sand Barrens, Oak Openings Metro Park, 1 Aug 2015, *Boone & Walters s.n.* (ISC – two sheets). **Mahoning Co.**: SW ¼ Berlin Twp., uncommon, small, very local, isolated population subjected to near full sun growing in small, shallow, wet depression within ca. 900 square-foot canopy opening in young, even-aged, privately-owned pin oak flatwoods adjacent W of Berlin Lake State Wildlife Area, 12 Aug 2018, *Riley 4213* (OS – six sheets). **Portage Co.**: Windham Twp., local in *Carex utriculata – Scirpus cyperinus* boggy meadow, 0.3 mi. W of Portage/Trumbull County Line, 0.1. mi S of boundary fence, Camp Ravenna Training & Logistics Site, 9 Jun 2010, *Gardner 6840* (ISC); Windham Twp., local, 7.5 square-meter-area on sphagnum hummocks in boggy swamp, 0.33 mi. W of Portage/Trumbull County Line, Camp Ravenna Training & Logistics Site, 7 Jun 2011, *Gardner 7060* (ISC – five sheets), *7061* (ISC – four sheets); Rootstown Twp., small, local population growing along SW side of trail, Triangle Lake Bog State Nature Preserve, Ravenna, 16 Jul 2013, *Riley 2814* (OS – three sheets); Charlestown Twp., local population growing in front of igloo 2-B-4, Camp Ravenna Joint Military Training Center, 1 Aug 2014, *Riley 3040* (KE – five sheets). **Trumbull Co.**: Southington Twp., pasture, border of woods, 10 Aug 1947, *Rood 2291* (KE); *ibid*, old pasture field, Braceville Twp., 7 Jun 1949, *Rood 2467* (KE – two sheets, MIN); Braceville Twp., locally common in open, wet meadow, LaBrae Athletic Club, Warren, 3 Jul 2013, *Riley 2815* (OS – five sheets).

This species, first collected in Ohio on 10 Aug 1947 in Trumbull County by Almon N. Rood (KE), was originally labeled as *Rubus argutus*. More than 50 years later (in 2011), it was also discovered at Camp Ravenna Joint Military Training Center in neighboring Portage County. Though known in Ohio from only the northeast corner of the state and a single site in the Oak Openings of Lucas County, where it occurs in the wet meadows, woodland edges, and fallow fields of the northeastern counties, it is sometimes locally abundant. The bright green primocanes bearing distinctly dense prickles make this member of section *Arguti* easy to identify even while dormant. West Virginia is the only other state in which this species is known to occur (Davis et al. 1969, Kartesz 2015).

63) ***RUBUS DEPAVITUS*** L.H. Bailey (Rosaceae) – Aberdeen dewberry. **Scioto Co.**: Union Twp., local, low-arching, tip-rooting species with short, ascendate, glandular pedicels located along S-

SW edge of logging road, Shawnee State Forest, 29 Jul 2017, *Riley 3967* (OS – three sheets), *3968* (ISC – two sheets); *ibid*, 22 Jun 2018, *Riley 4214* (OS – four sheets).

There is a single floricane specimen collected on 30 Apr 1991 in Green Twp., Scioto County (*J.S. McCormac 3486*) (MU) from "dry, cindery ground of RR embankment." This sample resembles *Rubus depavitus* and was even annotated as such by Widrlechner in July 2017. Unfortunately, without a corresponding primocane, this collection cannot be positively confirmed as either *Rubus depavitus* or the very similar *Rubus kentuckiensis* L.H. Bailey. Given its preference for dry, upland woods and open areas, *Rubus depavitus* is presumed to be widely overlooked and under-collected throughout the southern third of Ohio.

64) ***RUBUS FULLERI*** L.H. Bailey (Rosaceae) – Fuller's bristleberry. **Ashtabula Co.**: Dorset Twp., edge, E-facing thicket, Dorset Wildlife Area, 30 Jun 2001, *Stamp & Riccio 126.01* (CLM); growing in association with *R. hispidus* on Blakeslee silt loam in recent clearing on N and E sides of holding pond, along W edge of parking lot, Pymatuning State Park, 4 Jul 2016, *Riley 3615* (ISC – two sheets), *3617* (ISC), *3618* (ISC – five sheets). **Cuyahoga Co.**: abundant in wet acidic opening between SOM Center Rd. and Buttermilk Falls Pkwy., North Chagrin Reservation – Cleveland Metroparks; *ibid*, 25 Jun 2019, *Reinier 1796* (ISC – two sheets, KE – two sheets); *ibid*, 29 Jul 2019, *Reinier 1821* (ISC – two sheets, KE – two sheets). **Lorain Co.**: Frequent, disturbed, moist woods, city of Avon Lake, 25 Jun 1997, *Cusick 33893 & Schneider* (OS). **Portage Co.**: NE ¼ SE ¼ Windham Twp., rare and local, occurring on edge of wet, swampy woods along North Perimeter Fence, Camp Ravenna Joint Military Training Center, 17 Jun 2015, *Riley 3300* (ISC), *3301* (OS – two sheets); *ibid*, 24 Jun 2015, *Riley 3302* (KE – two sheets); *ibid*, 29 Jul 2015, *Riley 3303* (ISC – two sheets); SE ¼ SE ¼ Windham Twp., large, local population of growing along E edge of *Pinus strobus* plantation, Camp Ravenna Joint Military Training Center, 8 Sep 2015, *Riley 3304* (ISC – two sheets), *3305* (OS – three sheets); S ½ SE ¼ Windham Twp., somewhat large, local, population growing on moist somewhat poorly drained, shaded site located at corner of mature mesic to wet mesic, even-aged woods, Camp Ravenna Joint Military Training Center, 12 Jul 2016, *Riley 3616* (OS – six sheets); NE ¼ Ravenna Twp., rare, local, robust population growing on rich, loam, open site on mesic, E-SE facing slope, on W side/edge of overhead powerline clearing, Shaw Woods Working Lands Park, Ravenna, 1 Jul 2017, *Riley 3969* (OS – seven sheets), *3970* (KE – two sheets); S ½ SE ¼ Windham Twp., local population growing within small, shallow, open depression/poorly-drained site, Camp Ravenna Joint Military Training Center, 3 Jul 2017, *Riley 3971* (KE – two sheets). **Trumbull Co.**: SW ¼ Braceville Twp., native, locally scattered, growing on open, mesic site, along S side of North Perimeter Road, Camp Ravenna joint Military Training Center, 18 Sep 2015, *Riley 3306* (OS – three sheets), *3307* (ISC – two sheets); *ibid*, 7 Aug 2017, *Riley 3972* (CM – four sheets), *3973* (CLM – three sheets).

Rubus fulleri, a species with low-arching, tip-rooting canes, is in many ways similar to members of sections *Hispidi* (Rydb.) L.H. Bailey and *Setosi* (L.H. Bailey) L.H. Bailey, especially to *Rubus hispidus* L. and *Rubus wheeleri* L.H. Bailey, except for the fact that unlike those two species, *Rubus fulleri* is decidedly glandular along the primocane axis and on the pedicels of the inflorescence. Unlike *Rubus hispidus*, *Rubus fulleri* does not retain its obovate leaves of three to five leaflets throughout the winter. Where it occurs in Ohio, *Rubus fulleri* often grows in association with *Rubus hispidus*, typically on edges of high-quality wetlands and wet to rich-mesic acidic woods. According

to Allison W. Cusick (pers. comm.), the site at which the Lorain County collection was made has since been destroyed. Since 2018, *Rubus fulleri* has been listed in Ohio as State Endangered (ODNR 2018).

65) ***RUBUS FURTIVUS*** L.H. Bailey (Rosaceae) – openground bristleberry. **Ashtabula Co.**: Richmond Twp., growing on moist ground at edge of swamp, N edge of Pymatuning Lake, 12 Jun 1966, *Cusick 2321* (KE); *ibid*, common, swamp forest, 0.25 – 0.50 mi. N, Padanarum Area, Pymatuning State Park, 28 May 1977, *Cusick 16502* (KE); *ibid*, rare, small, local, non-robust, fruiting population encompassing ca. 400 ft.^{2} area occurring on rich, silt-loam soil of hummocks within densely shaded, mature, even-aged swamp woods, Padanarum Area, Pymatuning State Park, 20 Aug 2017, *Riley 3974* (OS – two sheets), *3975* (KE – two sheets), *3976* (ISC – two sheets).

Davis et al. (1967) reported little about this seldom seen or "furtive" bristleberry, other than to mention that at the time, it had only been collected from a few locations in Tompkins County, New York. Their report was mistaken; Bailey's type was from Van Etten, New York, which is actually in Chemung County (Bailey 1947). Aside from those specimens from Ashtabula County, efforts to locate any additional specimens collected in the 50+ years since the publication of Davis et al. (1967) have thus far proven futile. Based on this information, and the fact that the site where it occurs in Ohio is a very pristine, mature swamp forest in which several other northern endemics occur, we conclude that this species is truly rare and worthy of consideration for state listing in both New York and Ohio.

66) ***RUBUS HUMILIOR*** L.H. Bailey (Rosaceae) – humble blackberry. **Portage Co.**: Shalersville Twp., uncommon, two local mature individuals growing along edge of open, fallow field, Morgan Preserve, Shalersville, 17 Jul 2013, *Riley 2824* (OS – three sheets); *ibid*, 24 Jul 2013, *Riley 2825* (OS – three sheets); SE ¼ Freedom Twp., uncommon, local, healthy, somewhat low-arching, non-tip-rooting, population with primocanes 18 to 24-inches above ground growing on rich, mesic site where subjected to full sun, Camp Ravenna Joint Military Training Center, 22 Jul 2018, *Riley 4191* (ISC – five sheets), *4192* (OS – five sheets).

Rubus humilior appears to be a rather uncommon species, which Davis et al. (1969) erroneously classified as a member of section *Arguti* and lumped in synonymy under *Rubus uvidus* L.H. Bailey. The glandular inflorescences of *Rubus humilior* are evidence enough that it is best categorized as a member of section *Allegheniensis* (L.H. Bailey) L.H. Bailey. *Rubus humilior* is currently known to occur in northeastern Ohio and northwestern Pennsylvania from where the type specimen was collected. When encountered in the field, this low-arching blackberry, with its comparably small, ternate or quinate leaves and delicate, glandular racemiform inflorescences, bears a strong resemblance to a dwarf *Rubus allegheniensis*. While some collections are easy to discern, others exist which lack clear discontinuities between *Rubus allegheniensis* and *Rubus humilior*. One such intermediate Ohio collection was made southeast of Wooster in Wayne County, *H.A. & T. Davis 8786*, 29 Jun 1949 (CM – two sheets).

67) ***RUBUS INVISUS*** (L.H. Bailey) Britton (Rosaceae) – upland dewberry. **Athens Co.**: York Twp., section 8, common species growing in dry oak woods, Wayne National Forest, 17 Aug 2013, *Riley 2821* (OS – three sheets). **Butler Co.**: Hanover Twp., section 12, Hueston Farm and Forest Preserve, 2009, *Mathews 32* (MU). **Hocking Co.**: Perry Twp., section 36, locally common species along N-NE edge of upland oak woods along S edge and near SE corner of cemetery, Morgan Chapel

UM Church, Rockbridge, 24 Aug 2017, *Riley 3980* (OS – four sheets), *3981* (ISC – two sheets). **Jackson Co.**: Milton Twp., section 16, scattered, along woods, by edge of pond, 20 May 1981, *Spooner 615* (OS). **Lawrence Co.**: Decatur Twp., section 26, uncommon, small, local, low-arching population growing in full sun on dry, wooded ridgetop, Dean State Forest, 1 Sep 2014, *Riley 3042* (OS – four sheets). **Montgomery Co.**: Randolph Twp., section 3, 30 plants, dry, rocky hilltop above Stillwater River, 30' S of Miami County line, Pigeye Reserve, 17 May 1987, *Stine 67* (MU); *ibid*, 5 Jun 1987, *Stine 66* (MU). **Muskingum Co.**: on dry land, near Zanesville, 23 Jun 1947, *Bailey 355, 358-359* (BH); Rest Area along Interstate 70 West, E of Zanesville, 18 May 2014, *Vincent 16677* (MU). **Perry Co.**: Clayton Twp., section 20, locally common, growing along NE edge of forest access lane within dry, open (recently harvested) oak woods, 29 Jun 2013, *Riley 2823* (OS – three sheets); *ibid*, 10 Aug 2014, *Riley 3043* (ISC – four sheets). **Scioto Co.**: extreme S Nile Twp., local, rather shaded population growing on mesic site within young sweetgum-sycamore woods on E side of Moore Run Bridle Trail, Shawnee State Forest, 9 Jun 2018, *Riley 4224* (ISC – three sheets). **Vinton Co.**: Harrison Twp., section 22, small, local somewhat shaded population growing on E-facing edge of mature, dry, upland, oak-hickory forest, 26 Aug 2017, *Riley 3982* (ISC – three sheets).

Kartesz (2015) presented a distribution map depicting a collection from Lawrence County. The basis for this particular record was a 1950 collection made by Floyd Bartley (housed at CM). While this specimen falls within the range of variation for this species, it lacks a primocane, and, thus, we cannot confirm its identity. Notwithstanding, in 2014, Riley did collect this taxon in Lawrence County.

68) ***RUBUS KENTUCKIENSIS*** L.H. Bailey (Rosaceae) – Kentucky dewberry. **Tuscarawas Co.**: Wayne Twp., frequent, edge of railroad track, Dundee, 16 Jul 1967, *Andreas 292* (KE).

This species is very similar to the aforementioned *Rubus depavitus,* differing in that its primocane leaves are always three-foliolate with the terminal leaflet being wide-elliptic to rhomboid and abruptly shouldered (Widrlechner & Riley 2017).

69) ***RUBUS LEVICULUS*** L.H. Bailey (Rosaceae) - bottomland dewberry. **Adams Co.**: Green-Jefferson Twp. line, frequent, dry field, jct. of Lower Twin Creek and Sunshine Ridge Rds., 29 May 1980, *Cusick 20032* (KE, OS); SE Green Twp., large population growing on dry, open, sandy terrace on E edge of successional field, W side of Sandy Springs Cemetery, Sandy Springs, 6 Jul 2013, *Riley 2820* (OS – three sheets); *ibid*, 25 Jun 2016, *Riley 3619* (ISC – six sheets). **Hocking Co.**: 13 Jul 1971, *Noblick 499* (OS). **Jackson Co.**: Liberty Twp., 13 May 1934, *Bartley & Pontius s.n.* (OS); Franklin Twp., section 27, along Franklin Valley Road, 13 May 1981, *Spooner 600* (KE); Liberty Twp., section 16, locally common species growing on dry, open, ridgetop, recently clear-cut site, 28 Jul 2013, *Riley 2822* (OS – three sheets). **Lake Co.**: Jun 1928, *Beardslee s.n.* (OS). **Lawrence Co.**: Elizabeth Twp., sandy oak woods, 16 May 1969, *Silberhorn s.n.* (KE). **Lucas Co.**: Springfield Twp., section 6, moist, grassy field, Campbell Nature Preserve, 29 May 1987, *Cusick 26479* (MU). **Perry Co.**: Growing along abandoned RR tracks, old 12, 3 mi. south of Corning, 15 May 1965, *Perine 470* (BHO). **Ross Co.**: Green Twp., section 32, uncommon, small, local, somewhat depauperate population growing in acidic clay soil on open slope along N side of trail within dry, upland canopy opening, Great Seal State Park, Chillicothe, 19 Jun 2015, *Riley 3309* (OS – two sheets); western Franklin Twp., low-arching, tip-rooting population growing in canopy opening within mature, dry, upland (ridgetop) oak-hickory woods, Scioto Trail State Forest, 22 Jun 2018, *Riley 4225* (OS – three sheets), *4226* (ISC – two sheets); Harrison Twp.,

section 15, large population growing along either side of skid trail within small opening in mature, mesic, upland woods, Tar Hollow State Forest, 28 Jul 2018, *Riley 4227* (OS – six sheets). **Scioto Co.**: SE Nile Twp., small, local, somewhat depauperate population growing in small canopy opening on dry, acidic, nutrient poor, clay soil located on and along E side of skid trail on S-facing, upper slope within mature, upland oak-hickory woods, Shawnee State Forest, 22 Jun 2018, *Riley 4229* (ISC – three sheets). **Vinton Co.**: Vinton Twp., mixed oak woods, Vinton Furnace Experimental Forest, 15 May 2005, *Glasgow 37* (BHO).

Despite the common name given for this glandular dewberry with inflorescences with 1 to a few flowers bearing ascendate pedicels, it is typically found in Ohio in dry, upland, and sandy oak woods.

70) ***RUBUS MERACUS*** L.H. Bailey (Rosaceae) – dryslope dewberry. **Adams Co.**: dry ridge-top woods, along Sunshine Ridge, Edge of Appalachia Preserve, 19 Jun 2015, *Boone s.n.* (MU – two sheets). **Carroll Co.**: 30 Jul 1962, *Fuller & Fuller F-62-71* (MIL). **Erie Co.**: Sandusky, 31 May 190?, *Kellerman s.n.* (OS); Cedar Point, 29 Jul 1903, *Jennings s.n.* (OS); Berlin Twp., on brushy railroad embankment, w of Ceylon, 2 Jul 1971, *Jones 71-7-2-290* (OS). **Hamilton Co.**: oak woods on ridge-top, Bender Mountain, 27 Jun 2015, *Boone s.n.* (MU – two sheets). **Highland Co.**: East Monroe, 13 Jul 1899, *Kellerman s.n.* (OS). **Portage Co.**: extreme SE corner Windham Twp., uncommon, small, local, tip-rooting colony growing on slag of abandoned RR tracks where plants are subjected to half-full sun, Camp Ravenna Joint Military Training Center, 30 Sep 2016, *Riley 3614* (ISC – four sheets); *ibid*, 12 Jul 2017, *Riley 3983* (OS – four sheets); SE ¼ Windham Twp., somewhat large population growing on slag ballast along E edge of RR tracks near SE edge of East Classification Yard on dry, open site, Camp Ravenna Joint Military Training Center, 20 Jul 2018, *Riley 4230* (ISC – four sheets). **Trumbull Co.**: SE ¼ Farmington Twp., rather common and abundant dewberry growing on open, moist-mesic site within 100 ft. wide overhead powerline clearing, Grand River State Wildlife Area, 22 Jul 2018, *Riley 4231* (ISC – two sheets).

According to Davis et al. (1968), *Rubus meracus* is a relative of *Rubus roribaccus* (L.H. Bailey) Rydb. widely distributed in the Midwest; at times, these two taxa can be difficult to distinguish [see Widrlechner (2013)].

71) ***RUBUS MISSOURICUS*** L.H. Bailey (Rosaceae) – Missouri bristleberry. **Lorain Co.**: a tall (2 m) upright plant, among bushes in fencerow, Oberlin, 5 Aug 1948, *Grover 48-20* (BH – two sheets); *ibid*, 6 Aug 1948, *Grover 48-24* (BH – two sheets).

According to Widrlechner (2013), in Missouri, this member of section *Setosi* with its upright-arching primocanes and arching floricanes occurs in upland and bottomland prairies, edges of bottomland forests, streambanks, within pastures, and along fencerows. This plant has been found in similar habitats in eastern and southeastern Iowa and is an indicator of native prairies and savannas (Widrlechner 1998). Despite descriptions to the contrary, *Rubus missouricus* is not a tip-rooting species (Widrlechner 1998), one that is now known to occur as far east as Ohio.

72) ***RUBUS PLICATIFOLIUS*** Blanchard (Rosaceae) – plaitleaf dewberry. **Adams Co.**: Tiffin Twp., frequent in old field, Ohio Brush Creek Swirl Preserve, 17 May 2000, *Gardner 3051 & McCarty*

(OS). **Cuyahoga Co.**: Disturbed land N of Ridgewood Drive, ½ mi. W of the entrance road from Ridgewood Drive into West Creek Preserve, Parma, 27 Jun 2000, *Wilder & McCombs 13737* (SWF – two sheets). **Fulton Co.**: 8 Jul 1951, *Davis & Davis 9403* (MIL). **Geauga Co.**: Bainbridge Twp., roadside, Route 306 at Pettibone Rd., 5 Jul 1959, *Herrick s.n.* (OS). **Huron Co.**: Townsend Twp., on N.Y.C. RR track 3 mi. W of Wakeman, 18 Jul 1965, *Jones s.n.* (OS – two sheets). **Portage Co.**: Franklin Twp., roadside, Route 162, city of Kent, 6 Jul 1959, *Herrick s.n.* (OS); SW ¼ Deerfield Twp., locally common species growing within small canopy opening on SE side of grassy access lane, Dog Training Grounds/Public Hunting Area, Berlin Lake Wildlife Area, 13 Jun 2015, *Riley 3310* (OS – three sheets); *ibid*, 26 Jun 2015, *Riley 3311* (OS – five sheets); NE ¼ Charlestown Twp., small, local bramble growing on open, well-drained site along edge of woody brush on S side of range, Camp Ravenna Joint Military Training Center, 20 Jul 2018, *Riley 4232* (OS – four sheets).

Rubus plicatifolius is widely distributed from Iowa and Minnesota, east to Maine and southeastern Pennsylvania (Widrlechner 1998). This species is believed to be abundant throughout Ohio and should be sought in dry, open, somewhat disturbed areas and successional fields. The Cuyahoga County collection was originally reported by Wilder and McCombs (2002) as *Rubus recurvicaulis* Blanchard, based on Gleason and Cronquist (1991), who treated *Rubus plicatifolius* as a synonym of *Rubus recurvicaulis*.

73) ***RUBUS RECURVANS*** Blanchard (Rosaceae) – recurved blackberry. **Fulton Co.**: 8 Jul 1951, *Davis & Davis 9404* (MIL); *ibid*, 5 Jul 1962, *Fuller & Fuller F-62-13* (MIL). **Huron Co.**: 3 Jul 1949, *Davis & Davis 8769* (CM). **Ottawa Co.**: 23 Jun 1947, *Gordon 47-3* (BH); 23 Jun 1947, *Gordon 47-4* (BH). **Portage Co.**: SE ¼ Shalersville Twp., large, local population growing on open, well-drained, mesic site, Morgan Preserve, 23 Jul 2013, *Riley 2812* (OS – two sheets); *ibid*, 24 Jul 2013, *Riley 2813* (OS); *ibid*, 18 Jun 2015, *Riley 3312* (OS – four sheets). **Wayne Co.**: NW of Wooster on top of bank along Ohio 302, 5 Jul 1957, *Davis & Davis 11863* (CM).

In his distribution map, Widrlechner (1998) included Fulton and Ottawa Counties as having a confirmed collection of this species. Kartesz (2015) also cited Ottawa County, and also included Darke and Wayne Counties in the state distribution of this species. While we have recently verified the Wayne County record, we discovered that the Darke County record cited by Kartesz was based on Braun's (1961) acceptance of an incorrect identification.

74) ***RUBUS RORIBACCUS*** (L.H. Bailey) Rydb. (Rosaceae) – Lucretia dewberry. **Portage Co.**: SE ¼ Ravenna Twp., small, local population growing on dry, W-facing slope within mature, upland oak woods, Havre Woods Park, Ravenna, 4 Jul 2013, *Riley 2828* (OS – two sheets); *ibid*, 25 Jul 2013, *Riley 2829* (OS – three sheets); SW ¼ Windham Twp., locally abundant, large population on W edge of canopy opening within mature, rich, mesic sugar maple woods, Camp Ravenna Joint Military Training Center, 7 Jul 2015, *Riley 3292* (OS – six sheets); SW ¼ Windham Twp., locally abundant, large population growing in open, young successional brushy area on E side of abandoned RR lane, Camp Ravenna Joint Military Training Center, 9 Jul 2015, *Riley 3293* (OS – two sheets), *3294* (ISC – two sheets); *ibid*, 28 Jul 2015, *Riley 3295* (OS – three sheets).

Cooperrider et al. (2001) treated this species as a synonym of *Rubus flagellaris*, both of which lack stipitate glands on the pedicels. Given the widespread general habitat in which this species occurs, it is likely much more common throughout Ohio than these few records indicate.

75) ***RUBUS ROSA*** L.H. Bailey [syn. ***RUBUS ERIENSIS*** L.H. Bailey] (Rosaceae) – rose blackberry. **Erie Co.**: Near Hummel's Pond, Kelleys Island, 26 Jun 1947, *Gordon 47-5* (OS – two sheets). **Ottawa Co.**: Put-In-Bay Twp., South Bass Island, Lighthouse Point, canes arching to upright, in dense *Rhus typhina* thickets and along edge of road, 16 Jul 1970, *Duncan 1227* (OS).

Bailey's holotype of *Rubus eriensis* was collected in Ottawa County and is located at BH. Widrlechner (1998) examined this specimen and determined it to be synonymous with *Rubus rosa*.

76) ***RUBUS SATIS*** L.H. Bailey (Rosaceae) – ample dewberry. **Ashtabula Co.**: Kingsville Twp., uncommon and local, growing on N edge of mesic woods near ledge of steep bluff high above Lake Erie, Sunset Park, North Kingsville, 23 May 2015, *Riley 3313 & Beechey* (OS); *ibid*, 25 May 2015, *Riley 3314 & Beechey* (OS – three sheets); *ibid*, 5 Jul 2015, *Riley 3315 & Beechey* (OS – six sheets). **Ross Co.**: Along Seney Road, Camp Sherman, Chillicothe, 27 May 2005, *Godec CS035* (MU). **Seneca Co.**: Thompson Twp., 4 mi. W of Flat Rock, 13 Jun 1969, *Jones 69-6-13-498* (MU).

According to Widrlechner (1998), the range of this large, mounding dewberry extends from the Atlantic Coast west to eastern Minnesota, Iowa, and Missouri. Because of the "generic appearance" of this large, mounding non-glandular dewberry, the diverse habitats in which it occurs, and the fact that Ohio is situated in the middle of its rather large distribution range, this species is likely more common than these few records might suggest.

77) ***RUBUS SEMISETOSUS*** Blanch. (Rosaceae) – swamp blackberry. **Lucas Co.**: Swanton Twp., section 33, common, sand barrens, Oak Openings Park, 28 Jun 1982, *Cusick 21734* (OS); Monclova Twp., section 11, floricanes low & arching, but not tip-rooting, common, sandy opening, Toledo Express Airport, 13 Jun 1989, *Cusick 28181* (OS); dry open sand, Oak Openings MetroPark, 18 Jul 2015, *Boone s.n. & Walters* (MU); Pin oak forest with open to shrubby understory, Kitty Todd Preserve, Mancy Tract (TNC), 17 Jun 1995, *Walters 1995:079* (CLM).

Despite rather significant morphological differences, Alice et al. (2014) treated this softly pubescent member of section *Setosi* in synonymy with *Rubus setosus* Bigelow. At the western edge of its native range in Iowa and Minnesota (Widrlechner 1998; Widrlechner & Smith 2008), *Rubus semisetosus* is quite rare, restricted to relatively undisturbed sedge meadows, acidic prairies, and sandy savannas, typically on sites with high water tables. In Ohio, we suspect that it may be restricted to sandy oak openings near Toledo.

78) ***RUBUS SERISSIMUS*** L.H. Bailey (Rosaceae) – everbearing blackberry. **Butler Co.**: Roadside and edge of pond, Windisch Road, south of Allen Road, 27 Aug 2015, *Boone s.n.* (MU – two sheets); large colony of robust plants to about 6 feet tall, canes arching, at edge of pond on W side of road, Windisch Rd., S of West Chester, 1 Aug 2017, *Vincent 17697* (ISC – three sheets, MU – three sheets).

Sometimes treated in synonymy with *Rubus pascuus* L.H. Bailey, this species likely originated under cultivation, with many of the typical characteristics of Old-World blackberries, and may actually be a stabilized hybrid between a European and a North American species (Alice et al. 2014; Widrlechner 2013). We view it as an invasive threat. Recent discussions with local field botanists indicate that its range is spreading rapidly in Kansas and Missouri.

79) ***RUBUS STEELEI*** L.H. Bailey (Rosaceae) – Steele's dewberry. **Fulton Co.**: Swan Creek Twp., section 35, locally common species growing in abundance in open areas on dry, sandy soil, Windbreak Arboretum, Maumee State Forest, 23 Jul 2016, *Riley 3625* (OS – two sheets), *3626* (ISC – three sheets). **Holmes Co.**: Prairie Twp., section 15, frequent in RR ballast near TR 346, 15 Jun 1971, *Wilson 1788* (OS). **Mahoning Co.**: NW ¼ Milton Twp., small, local fruiting population located on wet-muddy soil at public fishing access site on N side of Lake Milton Tributary, Lake Milton Public Hunting & Fishing Area, 5 Sep 2014, *Riley 3047* (OS – four sheets). **Portage Co.**: NW ¼ Charlestown Twp., small, local population growing on E edge of West Perimeter Rd. on dry-somewhat moist site, roadside above W edge of large, open swamp, Camp Ravenna Joint Military Training Center, 3 Sep 2015, *Riley 3316* (ISC – three sheets); *ibid*, 13 Jul 2016, *Riley 3627* (OS – four sheets). **Ross Co.**: Scioto Twp., SW of Chillicothe, between Paint Creek and Alum Cliff Rd., Buzzard's Roost, 16 Jun 2004, *Vincent 11731 et al.* (MU). **Summit Co.**: south central Green Twp., S end of Singer Lake, just E of dam, 31 May 1979, *Andreas 3564* (MU). **Trumbull Co.**: Braceville Twp., Erie RR embankment, 14 Jun 1950, *A.N. Rood 2499* (KE); east central Braceville Twp., local population growing on dry, open, disturbed site (soil pile) on N side of gravel parking lot, LaBrae Athletic Club, Warren, 28 Aug 2015, *Riley 3317* (OS – two sheets). **Wood Co.**: Weston Twp., section 25, canes tip-rooting, prostrate, cinders on RR embankment, 20 May 1987, *Cusick 26413* (OS).

Though Widrlechner (1998) did not map a single county record of this species for Ohio, *Rubus steelei* has an extensive native range, from northeastern Texas to the Atlantic Coast, north to northern Minnesota and south to Alabama and Georgia. The habitats in which this glandless species occurs are diverse and abundant (Widrlechner 2013). Where it occurs in Ohio, this slender dewberry is rather weedy in habit.

80) ***RUBUS TRIVIALIS*** Michx. (Rosaceae) – southern dewberry. **Clermont Co.**: Over 100 plants, some flowering, on bank of Ohio River near boat ramp, Steamboat Bend Park, 22 Jun 2005, *Boone s.n.* (ISC, MICH, OS); growing on the rocky edge of the boat ramp and along the bank of the Ohio River, Woodland Mound Park, 11 Jun 2006, *Becus 61106* (OS); extreme W-SW corner of Pierce Twp., large population growing on NE bank of Ohio River, Woodland Mound Park, 7 Jul 2007, *Riley 771 & Boone* (MU), *772* (OS); *ibid*, 14 Jul 2007, *Riley 773* (OS), *774* (MU).

Braun (1961) cited her own voucher from Hamilton County, which was collected on 18 Oct 1916 from dry fields at Ellenora (Mt. Washington) and is housed at CINC. After a very long gap, this dewberry, which is very common in the southern US (Kartesz 2015), was rediscovered in Ohio by Dan Boone in 2004 along the Ohio River in neighboring Clermont County, not far from the Hamilton County line. Since 2016, *Rubus trivialis* has been listed in Ohio as State Endangered (ODNR 2018).

81) ***RUBUS ULMIFOLIUS*** Schott var. ***ANOPLOTHYRSUS*** Sudre (Rosaceae) – thornless elmleaf blackberry. **Hamilton Co.**: Growing in the edge of a woods, could be remnants of an old berry garden, east of Harrison, south of Harrison Avenue, 18 Jul 2008, *Boone s.n.* (ISC – two sheets).

The occurrence of *Rubus ulmifolius* in North America was treated by Alice et al. (2014), who give its current range as Washington, Oregon, California, and Nevada in the western USA. In contrast, within the eastern USA, it had only been reported from New Jersey, where it has not been collected since 1897 (Alice et al. 2014). Additional modern collection of var. *anoplothyrsus* [or more likely of horticultural cultivars derived from var. *anoplothyrsus* (Scott & Ink 1966; Clark & Finn 2008)] from eastern North America include *S. Ross 636*, 1 Jul 2000 from Mecosta County, Michigan (MICH) and *J.W. Johnson s.n.*, 13 Jun 2010 from Bruce County, Ontario (MICH).

82) ***RUBUS ULMIFOLIUS*** Schott × ***RUBUS*** ? (Rosaceae) – hybrid blackberry. **Portage Co.**: SE ¼ Windham Twp., small, local, escaped, low-arching, sterile population with tip-rooting primocanes growing on dry, open, grassy site and on slag ballast along E edge of RR tracks near SE side of East Class Yard, Camp Ravenna Joint Military Training Center, 14 Sep 2016, *Riley 3609* (OS – two sheets), *3610* (ISC – three sheets); *ibid*, 6 Jul 2018, *Riley 4237* (ISC – three sheets); *ibid*, 20 Jul 2018, *Riley 4238* (OS – four sheets); *ibid*, 8 Aug 2018, *Riley 4239* (ISC).

This sterile *Rubus ulmifolius* hybrid is a bit of a mystery – a mystery as to how it became established at this site and what the other parent may be. Pictures of this glandless taxa reviewed by Dr. Abraham "Bram" van de Beek (Leiden University), as well as specimens examined by co-author Widrlechner, lead them to believe that the diploid *Rubus ulmifolius* is clearly represented in this cross, but what the other parent is remains unknown. It was noted by Widrlechner that the narrow panicles of the inflorescences displayed in the 2018 vouchers are very suggestive of series *Vestiti* (Focke) Focke and not that of any North American species found in the region. Given this characteristic, along with its lack of stem hardiness within USDA hardiness zone 6 (USDA, ARS 2012) and its tip-rooting habit, this hybrid would most likely be classified within series *Vestiti*, adding even greater uncertainty as to its origin at this site.

83) ***RUBUS WHEELERI*** L.H. Bailey (Rosaceae) – Wheeler's bristleberry. **Portage Co.**: NW ¼ Paris Twp., rare, within shallow, seasonally wet depression on S edge of medium-aged, mesic woods, Camp Ravenna Joint Military Training Center, Ravenna, 9 Jun 2017, *Riley 3989* (OS); *ibid*, 3 Jul 2017, *Riley 3990* (OS – three sheets), *3991* (ISC – four sheets); *ibid*, 14 Jul 2017, *Riley 3992* (OS – four sheets); NE ¼ Paris Twp., small population within seasonally wet area, Camp Ravenna Joint Military Training Center, Ravenna, 3 Aug 2017, *Riley 3993* (KE – four sheets); NE ¼ Paris Twp., local, growing on moist, open site, Camp Ravenna Joint Military Training Center, 10 Aug 2018, *Riley 4236* (OS – three sheets). **Trumbull Co.**: SW ¼ Braceville Twp., local, growing on N edge of medium-aged, mesic-wet mesic pin oak flatwoods, Camp Ravenna Joint Military Training Center, 5 Jul 2017, *Riley – 3994* (OS – two sheets), *3995* (ISC – two sheets); *ibid*, 12 Jul 2017, *Riley 3996* (OS – two sheets), *3997* (ISC – two sheets); *ibid*, 13 Jul 2017, *Riley 3998* (KE – four sheets); *ibid*, 8 Aug 2017, *Riley 3999* (CM – four sheets), *4000* (CLM – four sheets).

Rubus wheeleri was first discovered in Ohio by Riley in 2017 at the Camp Ravenna Joint Military Training Center in Portage and Trumbull Counties. While it is a bit too early to comment on

its status in Ohio, it can be noted that, to date, *Rubus wheeleri* has only been found at four different sites, each along the edge of a young to medium-aged, mesic woods on somewhat poorly-drained soil. Variation for prickle density and presence of stipitate glands in these Ohio collections is somewhat greater than that reported for this taxon in Minnesota by Widrlechner and Smith (2008).

84) ***SCHOENOPLECTIELLA HALLII*** (A. Gray) Lye (Cyperaceae) – Hall's bulrush. **Pickaway Co.**: Circleville Twp., section 32, one plant in wet depression of agricultural field, Bartley Preserve, Circleville, 7 Aug 2011, *Boone 8-7-1230-11* (MO).

This obligate wetland sedge was recently discovered by Dan Boone in a prairie pothole wetland near Circleville, which happens also to be the only site in Ohio where its congener, *Schoenoplectiella saximontana* (Fern.) Lye occurs. As proposed by Smith and McKenzie (2011), *Schoenoplectiella hallii* is currently being reviewed for possible listing under the Endangered Species Act and has been designated as a Federal Species of Concern by the US Fish & Wildlife Service.

85) ***SIDERITIS MONTANA*** L. (Lamiaceae) – mountain ironwort. **Portage Co.**: Windham Twp., large, local, weedy population growing among slag ballast along E edge of RR tracks where plants receive full sunlight, Camp Ravenna Joint Military Training Center, 5 Jul 2017, *Riley 4016* (OS), *4017* (KE), *4018* (CLM); *ibid*, 7 Jul 2017, *Riley 4019* (OS), *4020* (MU), *4021* (CM), *4022* (BHO), *4023* (MICH).

Sideritis montana is "native in the region from southwestern Europe to Pakistan, including northern Africa. It rarely turns up in North America." (Go Botany 2018). According to Kartesz (2015) and Go Botany (2018), this annual has only been collected in one county in each of the following states: Arkansas (Fulton Co.), Connecticut (New Haven Co.), Nebraska (Dawes Co.), and South Dakota (Pennington Co.). We suspect that the Portage County population may have arrived on military vehicles returning from the Middle East.

SECTION II. DELETIONS

State Records

The following species have recently been determined to be non-native or never to have occurred in Ohio by the Ohio Rare Plants Advisory Committee, and/or by the authors of this paper based on specimen research, literature review, and consultation. Thus, the following species should be deleted from the Ohio flora for the reasons indicated below:

CASTANEA PUMILA (L.) Miller (Fagaceae) – dwarf chinquapin. A specimen at OS was collected by Floyd Bartley on 31 May 1953 from what was in all likelihood a cultivated plant near an old homesite not far from the Ohio River in Adams County. The label states that the sample was "collected in an open field 1 mi. S of Sandy Springs". The card catalog of Dr. E. Lucy Braun at OS includes a slip with information on a duplicate specimen housed at BHO. Efforts in 2018 by Dr. Harvey Ballard to locate this specimen were unsuccessful. No other herbaria searched in preparation of this paper have collections of *Castanea pumila* from outside of cultivation.

CRATAEGUS BRAINERDII Sargent (Rosaceae) – Brainerd's hawthorn. No valid specimen; all putative Ohio specimens were annotated in 2015 by Dr. James B. Phipps and Allison W. Cusick as not being *Crataegus brainerdii*. Ohio was not included within this species' range by Phipps (2014).

CRATAEGUS CHRYSOCARPA Ashe (Rosaceae) – fireberry hawthorn. This species was included as a native component of the Ohio flora in Cooperrider et al. (2001), but no valid, proof-positive specimen from within the state is known to exist. For this reason, Ohio was not included within this species' range by Phipps (2014). Some Ohio specimens of *Crataegus margarettae* Ashe and *Crataegus populnea* Ashe have historically been erroneously labeled as *Crataegus chrysocarpa*.

HALESIA CAROLINA L. (Styracaceae) – Carolina silverbell. Believed to have been collected from cultivation near New Boston, Porter Twp., Scioto County – based upon a vague label on a 1929 specimen at OS. A single, sterile specimen collected in Pike County in 1964 (also at OS) was later determined to be *Diospyros virginiana*. *Halesia carolina* has been planted ornamentally since the 1700s and is frequently cultivated in Ohio (Cooperrider 1995).

MALUS ANGUSTIFOLIA (Aiton) Michx. (Rosaceae) – narrowleaf crabapple. No convincing specimen with flowering or fruiting material is known to exist. Of the four Ohio counties from which this species was reported by Kartesz (2015), including Adams, Fairfield, Hocking, and Wayne, most putative specimens from these counties have been determined as *Malus coronaria* (L.) Mill. var. *lancifolia* (Rehder) C.F. Reed.

POPULUS DELTOIDES W. Bartram ex Marsh. var. ***OCCIDENTALIS*** Rydb. (Salicaceae) – plains cottonwood. No specimen. This taxonomic variety, reported from Ohio in Cooperrider et al. (2001), was reclassified by J.E. Eckenwalder (1977) as a synonym of *Populus deltoides* subsp. *monilifera* (Ait.) Eckenwalder.

RUBUS ORARIUS Blanch. (Roscaeae) – highbush blackberry, northern blackberry. It was included as native to the Ohio flora in Cooperrider et al. (2001), but no valid specimen from Ohio exists to support this claim. As discussed in Davis et al. (1969), *Rubus orarius* is only known from Hancock, Penobscot, and York Counties in coastal Maine. Fernald (1950) included it in synonymy with *Rubus pensilvanicus* Poir., although Davis et al. (1969) contended that it may be more closely aligned with section *Canadenses* (L.H. Bailey) L.H. Bailey than with section *Arguti* due to its rather glabrous leaf characteristics and prickles being few and short.

RUBUS RECURVICAULIS Blanch. (Rosaceae) – arching blackberry. Collected in Cuyahoga County and reported as new to Ohio by Wilder and McCombs (2002) following the taxonomic treatment of Gleason and Cronquist (1991), Widrlechner's recent examination of this specimen housed at SWF determined it to be *Rubus plicatifolius* (see Section I). As such, no valid records of *Rubus recurvicaulis* are known from Ohio.

RUBUS SETOSUS Bigelow (Rosaceae) – setose blackberry. No valid specimen. Cooperrider et al. (2001) included it based on two misidentified specimens at KE from Fulton and Trumbull Counties, which were later determined to be *Rubus hispidus* (*Cusick 11891*) and *Rubus densissimus* (*Rood 2291 & 2467*), respectively. Two interesting specimens from NASA Plum Brook Station in Erie County were collected in 1994: *Cusick 31745* (KE, OS) and *Cusick 31847* (OS). In 2002, Widrlechner

annotated these specimens, stating that they "fall within the range of variation of *Rubus s*ection *Setosi*, yet do not conform to the characteristics of described taxa. Perhaps they represent responses to repeated cutting or grazing". It is unknown to the authors if additional collections were made at this site, and if so, where they may be. Based on these notes and observations from 30 years of studying North American *Rubus*, it is clear that *Rubus setosus* is not a very common plant – one that is only known to occur east of Ohio.

STYRAX AMERICANUS Lam. (Styracaceae) – American snowbell. The erroneous Pike County, Ohio report cited by Kartesz (2015) is derived from Cooperrider (1995), which is based on a label mix-up for a specimen collected in North Carolina in 1965 by C.S. Johnson (*148*), a graduate student at the time. In 2002, the Ohio Rare Plant Advisory Committee discovered that this voucher, housed at NCU, was collected at Chimney Rock (presumably Chimney Rock State Park), North Carolina, and not at Chimney Rocks, Ohio, located in Pike County.

County Records

The following entries are miscellaneous county reports which are now known to be based on incorrectly identified specimens collected in the county(ies) identified in bold font for each respective species. These incorrectly identified specimens are included here in addition to those previously mentioned throughout this article. The determination of each was made by one or more of the authors of this paper based on specimen research, literature review, and consultation. Thus, the following species should be deleted from the respective county or counties indicated next to each:

CAREX HAYDENII Dewey (Cyperaceae) – Hayden's sedge. **Erie**, **Henry**, **Lorain**, **Lucas**, **Muskingum**, and **Trumbull Co.**: Aside from the introduced and naturalized collections found in Cuyahoga County referenced in Section I, all other Ohio material, labeled as such from each of the six aforementioned counties reported by Kartesz (2015), has recently been determined to be *Carex stricta* Lam. by either Dr. A.A. Reznicek or R.L. Gardner. This species is not known to naturally occur in Ohio and was therefore removed from the state's rare plant list in 2018.

CRATAEGUS COMPACTA Sargent (Rosaceae) – Thames hawthorn, clustered hawthorn. **Brown, Delaware, Franklin, Jackson, Lake,** and **Ross Co.**: Palmer (1956) reported Ohio collections from these six counties, however, once relocated, it was found that these specimens are not *Crataegus compacta*. Based on Palmer's article, Braun (1961) and Phipps (2014) included Ohio within the range of this species, and it is most likely the reason why Lance (2014) did as well.

CRATAEGUS PENNSYLVANICA Ashe (Rosaceae) – Pennsylvania hawthorn. **Clinton, Cuyahoga,** and **Franklin Co.**: Palmer (1956) and Braun (1961) reported this species from these three widely scattered counties. The specimens upon which these reports are based were found to be misidentified and have since been correctly annotated or, as is all too often the case with *Crataegus* vouchers, lack sufficient material to make a positive identification. In an April 2016 email correspondence with Mr. John Guccion, whose personal collection is cited in Braun (1961), he noted that he sent three sterile specimens (*J.G. Guccion 8-10*) from East Cleveland in Cuyahoga County to Dr. Ernest J. Palmer in 1953 for identification. In his response letter to Mr. Guccion, Dr. Palmer determined the sterile material to be *Crataegus pennsylvanica* but included a "?" next to his annotation due to the degree of his own uncertainty, adding "But fruit or flowers should be seen to make the determination certain." Dr. Palmer

did not return the samples to Mr. Guccion. Due to the absence of any other confirmed specimens, in Ohio, *Crataegus pennsylvanica* is currently only known to occur in Portage County. See entry in Section I.

CRATAEGUS SUBORBICULATA Sargent (Rosaceae) – Caughuawaga hawthorn. **Fairfield**, **Franklin**, **Lake**, **Ottawa**, and **Tuscarawas Co.**: E.L. Braun made an entry on an index card at OS of a specimen of *Crataegus suborbiculata* at the Horsey Herbarium collected in Ottawa County and determined as such by Dr. E.J. Palmer. There is some uncertainty over exactly where this collection was made, given that the index card reads Ottawa County, yet explicitly states that the specimen is from Toledo (in Lucas County). No other information about this collection is given and as such, extensive efforts to locate and verify it have been unsuccessful. Therefore, it is assumed that it has either found its way into another collection or, most likely, has since been reidentified and annotated as a morphologically similar taxon. As for the collections from Fairfield, Franklin, Lake, and Tuscarawas Counties reported by Kartesz (2015), the specimens upon which this information is based were labeled as *Crataegus kellermanii* Sarg., which is now regarded an interserial hybrid between *Crataegus pruniosa* (Wendl.) K. Koch. and *Crataegus punctata* Jacq. (Phipps 2014). For this reason, *Crataegus* ×*kellermanii* Sarg. is not to be treated as synonymous with *Crataegus suborbiculata*. However, based on our examination of these vouchers, they appear to represent one of the four recognized varieties of *Crataegus pruinosa* known to occur in Ohio. Due to the apparent absence of valid specimens upon which all prior reports were based, we agree with Phipps (2014) that, at that time, *Crataegus suborbiculata* was not known to occur anywhere in Ohio. See entry in Section I regarding the only verified collections of this species from Ohio, discovered in Portage County in 2016.

PRUNUS NIGRA Aiton (Rosaceae) – Canada plum. **Cuyahoga**, **Geauga**, and **Lawrence Co.**: While native to Ohio based on verified specimens from Lucas and Wood Counties, this state-endangered species has not been found to occur in any other county in Ohio. Braun (1961) reports an occurrence of *Prunus nigra* from Lawrence County based on a misidentified, unnumbered, sterile specimen collected by Floyd Bartley (OS) at Table Rock on 10 Jun 1951. Without question, this particular specimen is that of *Prunus avium* (L.) L., not *Prunus nigra*. In addition, Kartesz (2015) included Cuyahoga and Geauga Counties within the distribution of *Prunus nigra*. The specimens upon which this report is based are also incorrectly identified. *Prunus avium*, or sweet cherry, has been widely cultivated for centuries in North America for its delectable, fleshy fruits which are also sought after by wildlife, especially birds. For these reasons, *Prunus avium* can most likely be found as an escape in each of Ohio's 88 counties.

QUERCUS FALCATA Michx. (Fagaceae) – southern red oak. **Adams Co.**: Occurrence originally reported by Braun (1961) based on an unnumbered collection dated 6 Apr 1959 (OS) from "sandy soil, Ohio River terrace" in Sandy Springs, located in southeastern Adams County. The site at which this collection was made is at or adjacent to Sandy Springs Cemetery located on US Rte. 52 – a site very well known for its botanical diversity. Braun's specimen lacks key diagnostic characteristics of *Quercus falcata*. For instance, the mature leaves, though falcate, lack pubescence on the abaxial surface except for small hairy tufts in the vein axils. Furthermore, the buds on the dormant twigs included with Braun's specimen are large and very pubescent. Today, this area contains numerous, mature specimens of *Quercus velutina*, and not a single *Quercus falcata* has been found in this botanically well-explored area since Braun's collection. Based on the intermediate characteristics of Braun's specimen from

Adams County, it has been determined to be *Quercus* ×*willdenowiana* (Dippel) Zabel. In Ohio, native populations of *Quercus falcata*, a state threatened species, are only known from Gallia, Jackson, Lawrence, and Scioto Counties. In addition to Adams, *Quercus* ×*willdenowiana* has been collected from Jackson and Scioto Counties (Vincent et al. 2011).

RUBUS ALUMNUS L.H. Bailey [syn. ***RUBUS COREI*** L.H. Bailey] (Rosaceae) – oldfield blackberry. **Monroe Co.**: Braun (1961) reported a specimen from Monroe County; however, this specimen (OS Accession 20248) was annotated as *Rubus allegheniensis* Porter by co-author Widrlechner in 2000.

RUBUS ARGUTUS Link (Rosaceae) – sawtooth blackberry, southern blackberry. **Lake** and **Trumbull Co.**: Kartesz (2015) reported occurrences of this southern species from Lake and Trumbull Counties. The Trumbull County record is based on a 10 Aug 1947 collection by Almon N. Rood who gathered a sample that he erroneously labeled as *Rubus argutus.* This voucher, which was recently verified as *Rubus densissimus*, resides at KE. The basis of the Lake County record, however, is unknown as no such specimens from said county have been seen or verified by the authors. Given the absence of accurately identified material and the unlikelihood of this species occurring as far north as northeastern Ohio, this report cannot be verified or accepted.

It is worth mentioning that Braun's index catalog at OS noted two specimens collected in 1934 from Scioto County housed at BUT. One specimen collected on 14 May gives the location as "Copperhead Fire Tower, Shawnee State Forest," while the other collected on 19 May states "1 mi. W of Otway." After relocating these specimens, which sampled only floricanes, we could determine neither of them beyond section *Arguti*. Consistent with our findings, Braun (1961) did not recognize the legitimacy of these records as *Rubus argutus* and simply indicated "no specimens."

RUBUS CANADENSIS L. (Rosaceae) – Canadian blackberry, smooth blackberry. **Mahoning Co.**: Cooperrider et al. (2001) included this eglandular species as native to the Ohio flora, while Kartesz (2015) reported collections from three Ohio counties including Cuyahoga, Lake, and Mahoning. In preparation for this paper, the authors tracked down the specimens upon which these reports were based and found all three to be incorrectly identified. The Cuyahoga and Lake County specimens, both housed at CLM, were determined to resemble *Rubus plicatifolius* although their true identity cannot be fully verified due to incomplete material. The Mahoning County voucher, which only includes floricane material, appears to be that of either *Rubus aboriginum* or *Rubus roribaccus*. This collection also resides at the Herbarium of Cleveland Metroparks. See entry in Section I for details concerning verified collections of *Rubus canadensis* made in 2019 from Cuyahoga and Lake Counties.

RUBUS RORIBACCUS (L.H. Bailey) Rydb. (Rosaceae) – Lucretia dewberry. **Erie** and **Highland Co.**: Kartesz (2015) included Highland County in the statewide distribution of this species, which is based on what appears to be an error in Cusick & Silberhorn (1977), who cite a Highland County (abbreviated therein as "HI") collection of *Rubus roribaccus*, adding "one record, reported by Braun (1961)" when in fact the only *Rubus roribaccus* specimen cited by Braun (1961) is from Erie County – not Highland County. In addition, no complete or positively identifiable collections of *Rubus roribaccus* from Highland County were found while searching for valid records to reference in Section I. The Erie County specimen mentioned by Braun is reported to be at OS (Accession 20283) and was collected in Sandusky on 31 May 190?. Widrlechner determined it to be *Rubus meracus*, while two

1895 collections from Erie County (*W.A. Kellerman s.n.*) and (*E.L. Mosley s.n.*) housed at OS lack sufficient material from which a positive identification could be made. Due to the incorrect identification of the former two specimens and the questionable determinations of the 1895 specimens (based on incomplete material), Widrlechner (1998) did not report a single county occurrence for Ohio. Included within *Rubus roribaccus* is *Rubus michiganensis* (Card ex L.H. Bailey) L.H. Bailey, a name which has been applied in a confusing manner. According to Widrlechner (1998), the type specimen of *Rubus michiganensis* fits within the range of variation of *Rubus roribaccus.* However, many other collections that Bailey considered to be *Rubus michiganensis* were actually *Rubus curtipes*. Kartesz (2015) mapped Huron and Wayne Counties for *Rubus michiganensis*. However, we have determined that specimens housed at CM that served as the basis for those county records were misidentified.

RUBUS TRIVIALIS Michx. (Rosaceae) – southern dewberry. **Geauga Co.**: Kartesz (2015) cited a collection from Geauga County, yet no voucher was ever found to substantiate this report. Upon looking into this questionable matter, Widrlechner learned that the basis for this citation is an unpublished manuscript on the Flora of Ohio written in 1991 by Dr. John J. Furlow. Due to absence of a valid specimen, we do not accept any reports of this species having been collected from or present in Geauga County.

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FIRST REPORT OF *AESCULUS FLAVA* (SAPINDACEAE) ADVENTIVE IN NEW YORK

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ABSTRACT

The Yellow Buckeye, *Aesculus flava* (Sapindaceae), is naturalized in Bronx and Putnam counties, New York. This report documents two large populations of spontaneous trees, one in each county and each consisting of numerous mixed-age individuals ranging from fruiting adults to saplings. Both populations occur in natural stands of mostly native tree species but are near homes and gardens. The plants are documented with herbarium specimens and iNaturalist observations.

This is the first report of the spontaneous occurrence of *Aesculus flava* Sol. (Sapindaceae) in New York (Werier 2017; Weldy et al 2019).

Voucher specimens. **New York.** Putnam Co.: Between towns of Garrison and Cold Spring and between the Hudson River and Rout 9D, in valley of Indian Brook, 79 Indian Brook Rd. at intersection with Warren Landing Road, 41.404333, -73.934347 (WGS84, ±25m), ca 52 m elev., 18 Aug 2019. *Atha 16072* (NY). Bronx Co.: New York City, grounds of the New York Botanical Garden, E of the Bronx River and N of the Stone Mill road, between the Lilac collection and the operations yard, 40.860210, -73.873225 (WGS84, ±25m), ca 22 m elev., 8 May 2018, *Atha 16002* (NY).

The Putnam County population consists of at least eight mature fruiting individuals of various size classes and numerous saplings scattered over approximately 0.5 hectares. The forest is dominated by *Acer rubrum*, *Acer saccharum*, and *Fagus grandifolia*. The Bronx County population consists of numerous fruiting trees of various size-classes and numerous saplings within an area of approximately 4 hectares in the Bronx River Forest, north of the New York Botanical Garden. The forest is dominated by *Fraxinus pennsylvanica, Fraxinus profunda, Morus alba, Acer platanoides, Acer saccharum, Acer negundo, Quercus rubra, Aesculus flava*, and *Celtis occidentalis*.

In addition to the specimens cited here, both populations are documented by observations in the community science program iNaturalist (iNaturalist 2019). The New York Botanical Garden voucher cited here (Fig 1) is from a solitary spontaneous tree located 1.1 km SSW of the Bronx River Forest population. The Putnam County voucher specimen is a fruiting collection.

Aesculus flava is native to the Appalachian mountains of northern Alabama and Georgia, north to southwestern Pennsylvania and the Ohio River Valley (Williams 1990). Its northward migration is not unexpected as the climate warms, but the fruit are heavy and not naturally dispersed long distances, except by gravity and water. More study may reveal naturally dispersed trees from southwestern Pennsylvania into New Jersey and toward New York, but the Hudson River, New York Bay, and the dense development of New York City are formidable barriers that would likely prevent natural dispersal. These dispersal dynamics and the observed pattern of spontaneous occurrence suggest that spontaneous individuals in New York are most likely dispersed locally from cultivated trees.

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Figure 1. *Aesculus flava* from a spontaneous tree in Bronx County, New York. *Atha 16002* (NY).

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DOCUMENTING A *SOLIDAGO BRENDAE* × *S. SEMPERVIRENS* HYBRID FROM THE GASPÉ, QUEBEC (ASTERACEAE: ASTEREAE)

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ABSTRACT

A collection from Mont-Louis, northern Gaspé, Québec, was originally identified as *Solidago canadensis* × *S. sempervirens*, but the location is outside the range of the first putative parent species. *Solidago brendae* does occur along the north shore of the Gaspé. A multivariate analysis of 61 specimens of *S. brendae*, *S. canadensis*, and *S. sempervirens* and the putative *S. brendae* × *S. sempervirens* specimen was performed and confirmed that *S. brendae* and *S. sempervirens* were the likely parents of the hybrid

During the process of examining and annotating all collections of *Solidago* in the Marie-Victorin Herbarium at the Jardin botanique in Montréal, (MT; Theirs continuously updated), a specimen identified as *Solidago canadensis* L. × *S. sempervirens* L. was encountered: *Labrecque & Lamoureux s.n.* (MT, Figs. 1-2; cited below). The collection site is on the northern shore of the Gaspé Peninsula, which is north of the range of *S. canadensis* but within the range of *S. brendae* Semple (Semple 2013; Semple et al. 2013; Semple 2019 frequently updated). Therefore, the possibility that one of the putative parents was not *S. canadensis* but *S. brendae*, which was only described in 2013, seemed more likely.

The second putative parent, *Solidago sempervirens*, is a member of subsect. *Maritimae* (Torr. & A. Gray) G.L. Nesom, which includes species with basal rosette and lower stem leaves that are generally much larger than upper stem leaves and have petioles that sheath the lower stem (Semple & Cook 2006). *Solidago brendae* and *S. canadensis* are members of subsect. *Triplinerviae* (Torrey & A. Gray) G.L. Nesom, which generally have secund pyramidal shaped inflorescences and lower stem leaves that are not the largest and usually not present at flowering. Also, lower and often mid and upper stem leaves of species of subsect. *Triplinerviae* have two prominent lateral veins that arise partway along the midvein; this is the "triple-nerved" condition of the subsection's epithet.

Labrecque & Lamoureux s.n. was borrowed from MT and morphological traits scored for inclusion in a multivariate analysis of *Solidago brendae*, *S. canadensis* var. *canadensis*, and *S. sempervirens* specimens. The results of the analysis are present below.

Materials and methods

In total, 62 specimens from MIN, the J.K. Morton personal herbarium now deposited in TRT, UNB, and WAT in MT (Thiers, continuously updated) were selected for inclusion in the analysis of of *Solidago brendae* (27 specimens), *S. canadensis* (21 specimens) and *S. sempervirens* (13 specimens), and one putative specimen of *S. brendae* × *S. sempervirens*. All traits scored are listed in Table 1. Specimens of *S. brendae* came from New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, and Québec. Specimens of *S. canadensis* (var. *canadensis* only) came from Maine, Massachusetts, New Brunswick, New York, Nova Scotia, Ontario, Québec, and Vermont. Specimens of *S. sempervirens* came from Delaware, Louisiana, Michigan, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Québec. Multivariate data on specimens of *S. brendae* and *S. canadensis* were selected from specimens previously used in Semple et al. (2013).

Figure 1. *Labrecque & Lamoureux s.n.* (MT); *Solidago brendae* × *S. sempervirens* from Mont-Louis, northern Gaspé, Québec.

Figure 2. Details of *Labrecque & Lamoureux s.n.* (MT); *Solidago brendae* × *S. sempervirens*. **A-B.** Lower and mid stems. **C.** Lower stem leaf. **D-F.** Mid stem leaf, margin, and proximal abaxial surface. **G-H.** Upper stem leaf and raised veins on abaxial surface. **I.** Heads. Scale bar = 1 cm in A-B, E, and H-I; = 1 mm in C-D and F-G.

Table 1. Traits scored for the multivariate analyses of *Solidago brendae*, *S. canadensis*, and *S. sempervirens* and one specimen of *S. brendae* × *S. canadensis*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip(cm)
BLFLN	Basal leaf length measured from the leaf base to tip(mm)
BLFPETLN	Petiole length of basal leaf- measured from the petiole base to tip of basal leaf (mm)
BLFWD	Basal leaf width measured at the widest point (mm)
BLWTOE	Basal leaf measured from the widest point to the tip(mm)
BLFSER	Basal leaf dentation-number of serrations of basal leaf
LLFLN	Lower leaf length measured from the leaf base to tip(mm)
LLPLETLN	Petiole length of lower leaf- measured from the petiole base to tip of the lower leaf (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end(mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip(mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end(mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPWD	Width of inflorescence (cm)
CBRNCHLN	Length of longest lower inflorescence branches (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
IPHYLN	Inner phyllary length (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
RPUB	Number of pubescence per ray achene (mm)
DCORLN	Disc corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc corolla lobe length lobe (mm)
DACHLN	Disc achene length (mm)
DPAPLN	Disc pappus length (mm)

Voucher, *Solidago brendae* × *S. sempervirens*. **Québec**. M.R.C. Denis-Riverin, Mont-Louis, près du pont sur la rivière {near the bridge on the river}, haut de rivage rocheux ave les deux parents présumés, également aven {rocky shoreline with both suspected parents, also with} *Cynoglossum officinale* et *Aster novi-belgii*, 6 Aug 1994, *Labrecque & Lamoureux s.n.* (MT). Figures 1 and 2.

Not all traits scored were included in the analyses. Traits used to define a priori groups were not included in the analyses to avoid circular logic. Differences in lower stem leaf traits were used to define a priori groups in part. Specimens of *S. sempervirens* usually had lower stem leaves that were the largest on the shoot. Specimens of *S. brendae* and *S. canadensis* lacked lower stem leaves and therefore traits on lower stem leaves were excluded. A Pearson pairwise correlation matrix was generated and only one trait of a pair of traits with a correlation value $|r| > 0.7$ was included in the analyses. The analyses included the following traits: mid leaf length, width, and number of margin serrations, upper leaf length, width, and number of margin serrations, involucre height, numbers of ray and disc florets, and disc floret corolla length.

Solidago brendae and *S. canadensis* do not produce basal rosettes during the flowering season and usually lower stem leaves have senesced at flowering; all traits for basal and lower stem leaves were not included in the analysis because inclusion would have resulted in only individuals of *S. sempervirens* being included. All individuals of *S. sempervirens* have lower stem leaves that partially or fully sheath the stem, while the lower stem leaves of *S. brendae* and *S. canadensis* do not sheath the stem.

The single analysis was performed using SYSTAT v.10 (SPSS 2000) following the methods of Semple et al. (2013). STEPWISE discriminant analysis was used to select traits that most strongly separated the three a priori groups in N-dimensional hyperspace. Classificatory discriminant analyses were run to place a posteriori the single hybrid specimen into one of the three a priori species level groups.

Results

In the STEPWISE discriminant analysis of three species-rank a priori groups *S. brendae*, *S. canadensis* and *S. sempervirens*, the following four traits listed in order of decreasing F-to-remove values were selected (F-to-remove): involucre height (67.28), number of ray florets (55.84), number of disc florets (29.61), and upper leaf length (7.46). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances between group centroids indicate the largest separations were between *Solidago brendae* and *S. sempervirens* (131.122) and between *S. canadensis* and *S. sempervirens* (130.623). The smallest separation was between *S. brendae* and *S. canadensis* (34.737).

Table 2. Between groups F-matrix for the three a priori group analysis (df = 11, 38).

Group	*brendae*	*canadensis*	*sempervirens*
brendae	0.000		
canadensis	34.737	0.000	
sempervirens	131.122	130.623	0.000

Lambda = 0.0210 df = 4 2 54 Approx. F= 75.3145 df = 8 102 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups *Solidago brendae*, *S. canadensis*, and *S. sempervirens* the percents of correct classification were all 100% for all three species. The Classification matrix and Jackknife classification matrix are presented in Table 3. All 13 specimens of *S. sempervirens* a priori group were placed a posteriori into *S. sempervirens* with 100% probability. All 27 specimens of the *S. brendae* a priori group were placed a posteriori into *S. brendae* group: 18 specimens with 100% probability, 7 specimens with 92-99% probability, 1 specimen with 82% probability, and 1 specimen with 72% probability (28% to *S. canadensis*). All 17 specimens of the *S. canadensis* a priori group were placed a posteriori into *S. candensis* plus 4 additional specimens included only a posteriori; 14 specimens with 100% probability and 7 specimens with 96-99% probability. Two specimens of *S. canadensis* not included a priori were placed a posteriori into *S. brendae* with 75% probability each. The single putative *S. brendae* × *sempervirens* specimen was placed a posteriori into *S. brendae* with 100% probability.

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of five a priori groups; a posteriori placements to groups in rows.

Linear classification matrix

	brendae	***canadensis***	***sempervirens***	% correct
brendae	27	0	0	100%
canadensis	0	17	0	100%
sempervirens	0	0	13	100%
Total	27	17	13	100%

Jackknifed classification matrix

	brendae	***canadensis***	***sempervirens***	**% correct**
brendae	27	0	0	100%
canadensis	0	17	0	100%
sempervirens	1	0	12	92%
Total	28	17	12	98%

A two dimensional plot of CAN1 versus CAN 2 canonical scores for 62 specimens of *Solidago brendae, S. canadensis*, *S. sempervirens*, and the single collection of *S. brendae* × *S. sempervirens* are presented in Fig. 3. Eigen values on the first two axes were 12.059 and 2.653.

Discussion

The results or the analysis plus the character states of several traits not included in the multivariate analysis support the revised identification of the *Labreque & Lamoureux s.n.* (MT) as *Solidago brendae* × *S. sempervirens,* not the original identification as *S. canadensis* × *S. sempervirens*. Because a single specimen cannot be treated as an a priori group in discriminant analyses, the hybrid specimen was not assigned to an a priori group but was included in the a posteriori classificatory discriminant analysis, which assigned the specimen a posteriori to *S. brendae* with 100% probability (0% to *S. canadensis*). On this result, the putative hybrid could be rejected as a hybrid. However, in the canonical discriminant analysis (a dimension reduction technique), the first and second canonical scores for the hybrid place the hybrid specimen at the periphery the *S. brendae* cluster of specimens, on the *S. sempervirens* side of the cluster and not on the side closer to *S. canadensis* (Fig. 3). A more traditional scatter plot diagram (e.g., see Fig. 13 in Semple and Semple 1977) could have been constructed and would have allowed the inclusion of traits that could not be included in discriminant analyses. Like all specimens of *S. sempervirens*, *Labreque & Lamoureux s.n.* (MT) had lower stem leaves with petioles that sheathed or partially embraced the lower stem

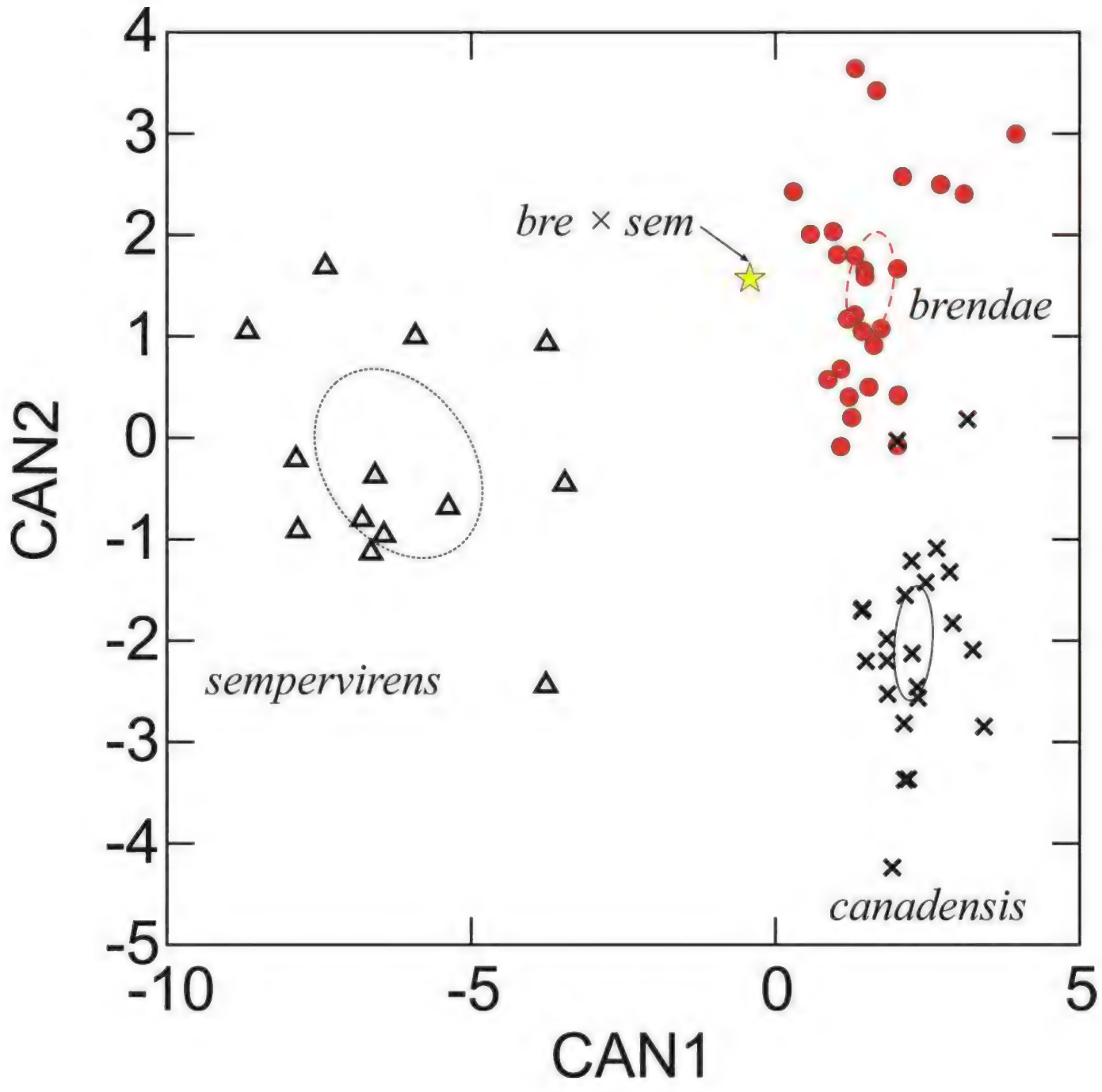

Figure 3. Plot of CAN1 versus CAN2 of specimens of *Solidago brendae* (red dots), *S. canadensis* (red triangles; position of *Hinds 3828* UNB indicated by P2), *S. canadensis* (black ×), *S. sempervirens* (black open triangles) and a *S. brendae* × *S. sempervirens* specimen (yellow star).

(Figs. 2A and 2C). Also, the lowest leaves still present on the stem of *Labreque & Lamoureux s.n.* (MT) had only 2-3 serrations per side while those of *Solidago sempervirens* had none and those of *S. brendae* and *S. canadensis* have multiple serrations on lower stem leaves (data are limited due to general absence of lower stem leaves on *S. brendae* and *S. canadensis*). The triple-nerved condition of the hybrid mid and upper stem leaves is obvious (Figs. 2D-E), but venation was raised and not like that of *S. brendae* and *S. canadensis*.

There is also the possibility that the hybrid specimen is not an F1 but is an F2 backcross of an F1 individual with the *Solidago brendae* parent. Such a specimen would have more traits in common with *S. brendae* than the hybrid. No experimental hybrids were created as part of this analysis.

Chromosome numbers reported for *Solidago brendae*, *S. canadensis*, and *S. sempervirens* are all diploid $2n=18$ (Semple 2019). Hybridization would be facilitated by the parents having the same ploidy level. Also, the lack of known polyploids in the three species means that ploidy level was not a factor in differences between morphological traits of the three species and the hybrid.

My conclusion is that Labrecque and Lamoureux did collect an interspecific hybrid in 1994 but they were understandably wrong in assuming it was a cross between *S. cana*densis and *S. sempervirens*. *Solidago brendae* was not described until recently (Semple 2013) and would not have been an option as a parent at the time the collection was made and originally identified. Documenting

statistically or experimentally the occurrence of interspecific hybridization in *Solidago* needs to be done for multiple other putative cases.

Comment on the species epithet of Brenda's Goldenrod

The species epithet for Brenda's Goldenrod was first published as *S. brendiae* because the author and the honorée liked the sound of the name with an "i" included. This was considered by nomenclatural authorities as not appropriate for a feminine name in Latin based on the name "Brenda" and *S. brendae* was listed on IPNI.org. *Solidago juliae* Nesom includes the "i" because the name "Julia" (and the diminutive, "Julie") is Latinized by dropping the "a" and adding the generative ending "-ae". Some journals insist on using only tyrannically imposed formal Latinized names while others have accepted that the original author of the name deliberately included an extra syllable as a matter of auditory preference. In this publication, the author of the epithet begrudgingly bows to the strict rules of Latinizing feminine names as mandated by the International Code of Botanical Nomenclature (Turland et al. 2018).

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COMPARISON BETWEEN TWO SURVEYS OF *PHYSOSTEGIA CORRELLII* (LAMIACEAE) IN TRAVIS COUNTY, TEXAS

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ABSTRACT

This study documents the results of distributional surveys conducted in 2014 and 2018 for the rare *Physostegia correllii* at Lady Bird Lake in Travis Co., Texas. Survey results showed that some *P. correllii* colonies were lost in between surveys but additional colonies were observed at new locations along deposited silt and sediment banks. Survey results indicate that the species is a stream bank specialist and disturbance fugitive preferring newly deposited and saturated sediment as well as sparse or low growing riparian vegetation to proliferate.

Physostegia correllii Lundell (Shinners), Correll's false dragonhead, is a rare, potentially threatened or endangered plant species found at scattered localities across southern and central Texas, coastal Louisiana, and northern Mexico (Cantino 1982). Plants are perennial, erect, horizontally rhizomatous herbs growing 1 meter or more tall. They have been observed growing along the edge of streams, ditches, and rivers (Poole et al. 2010) and the species perhaps had a more widespread distribution along springs and creeks of central Texas before urbanization.

The species is listed as critically imperiled in Louisiana (S1) and imperiled in Texas (S2). Historically *Physostegia correllii* has been noted or collected in 6 to 10 counties in Texas (Cantino 1982; Poole et al. 2010) and 4 parishes in Louisiana (Louisiana Natural Heritage Program 2010).

Figure 1 shows the distribution of *Physostegia correllii* in the USA (Kartesz 2015). The current status of *P. correllii* in many of these counties is unknown and the species is presumed to be extirpated from at least one Texas county (Poole et al. 2010). However *P. correllii* has continually been noted and observed in Travis County since it was first collected in 1952 along the Colorado River east of Austin. Over the last 10 years, observations have been made at sites along the shore of Lady Bird Lake just upstream of the original Travis County collection. Until 2014 no thorough surveys had been conducted at Lady Bird Lake to record localities other than the few previously known. We conducted a shoreline-based survey of the lake in order to document the number of *P. correllii* colonies and their growth habits.

Lady Bird Lake is a municipal reservoir located on the Colorado River as it passes through the city of Austin. The reservoir covers 190 hectares and is predominantly urban riverine habitat with multiple urban streams and storm water runoff channels flowing into it. Although Lady Bird Lake is highly modified aquatic habitat, it has a robust aquatic plant community and some areas of intact riparian communities. Water quality in Lady Bird Lake is generally good (City of Austin 2011).

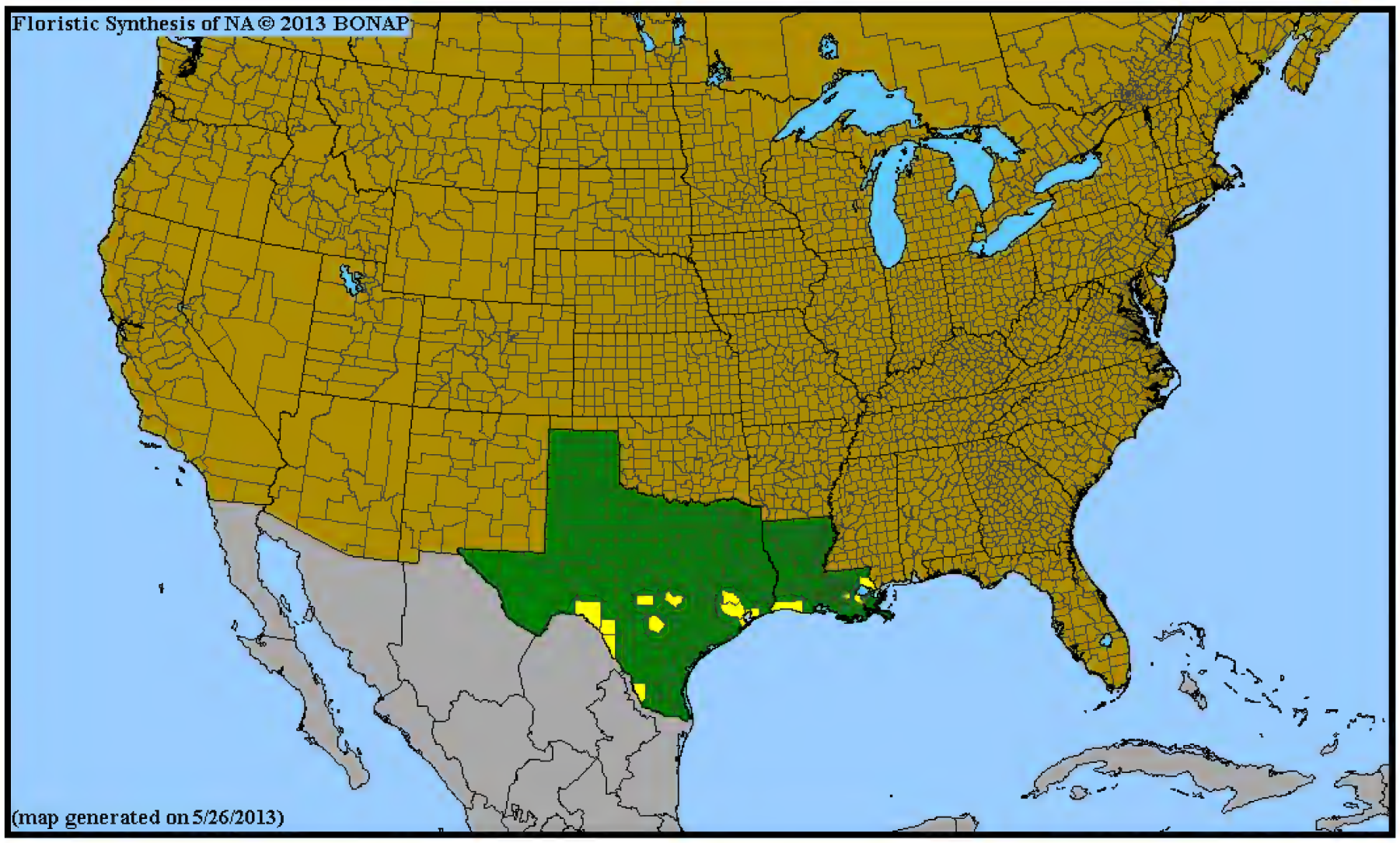

Figure 1. County distribution of *Physostegia correllii* in the USA (Kartesz 2015).

The reach of the Colorado River impounded to form Lady Bird Lake has historically been fed by several springs and spring fed tributaries. These include Barton Creek, which is fed by the fourth largest spring system in Texas. Barton Springs, Deep Eddy Springs, Bee Springs, Durham Springs and Seiders Springs all once provided perennial sources of water in the vicinity (Brune 1981). Many of these springs and tributaries are now surrounded by urban growth and have little to no intact riparian or aquatic habitat.

Methods

From April to September 2014 and April to August 2018 the survey team utilized kayaks to conduct this survey. Since *Physostegia correllii* typically grows along the edge of water, utilizing kayaks provided a clear line of site to colonies that would otherwise be hidden when viewing from the bank. A hand-held gps unit (Garmin or Trimble) or a cellular phone application (Polaris Navigator) was used to collect GPS coordinates. Latitude and longitude (D:M:S) were recorded and entered into a data sheet along with a point number. For data collected by cellular phone, GPS Earthpoint tools for Google Earth was used to convert these coordinates into a Google Earth layer. For Garmin or Trimble machines, collected data points were downloaded and converted into an ARC GIS shapefile. In addition to coordinates, other data such as soil type, colony length, colony width, maximum height of colony, stem counts, canopy density, and associated herbaceous and riparian species were also collected.

Results

During the 2014 survey 22 colonies of *Physostegia correllii* were found growing along the shoreline of Lady Bird Lake and one colony was located on an island situated in the Colorado River 70 meters below Longhorn dam. During the 2018 survey, 8 of the 2014 colonies were not relocated, including the Colorado River colony. However, 8 colonies were found at new locations, bringing the total number of colonies in 2018 back to 23. Figure 2 illustrates the difference in colony distribution between 2014 and 2018 surveys.

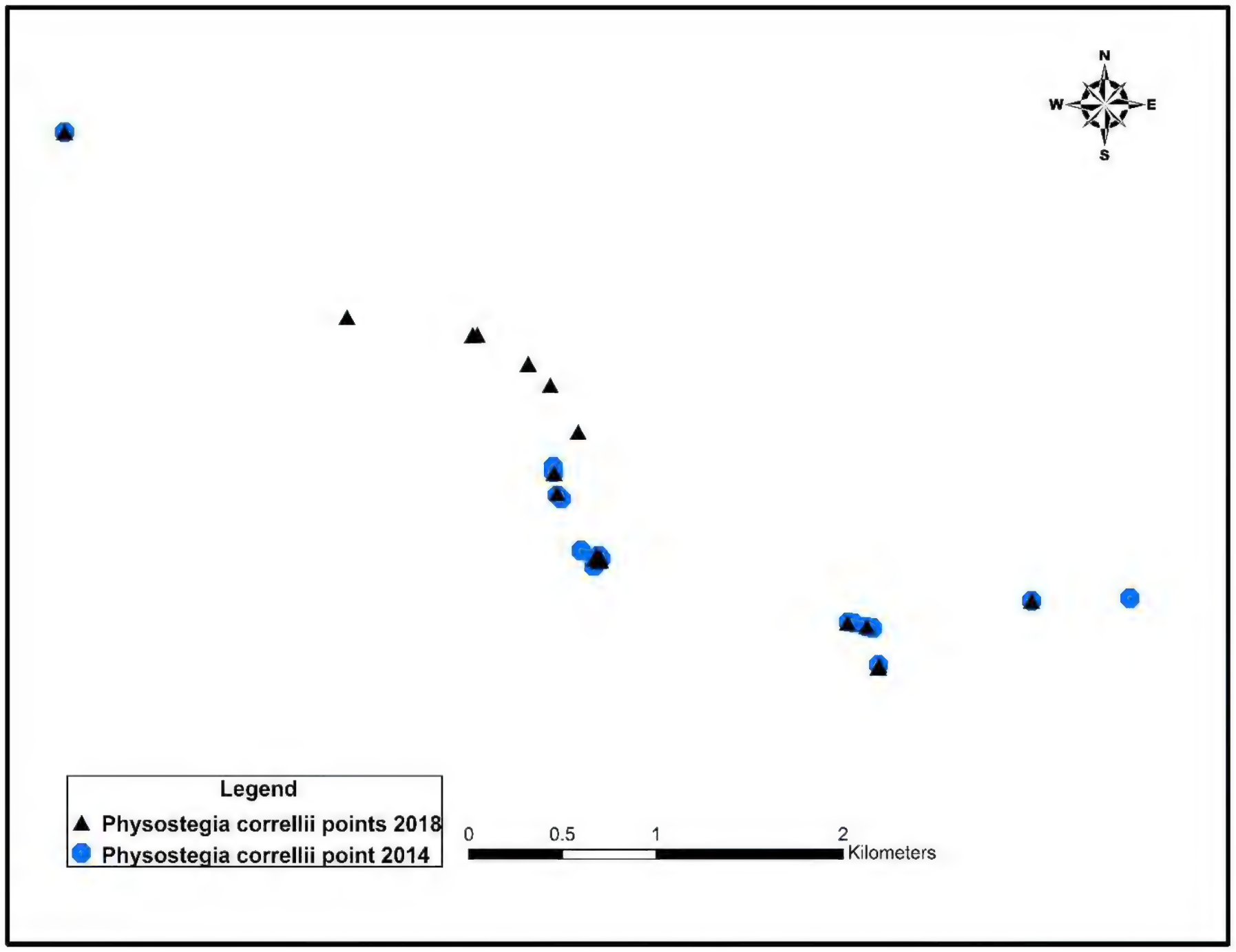

Figure 2. Distribution of *Physostegia correllii* colonies in 2014 and 2018. No specific geographic locations or topography are provided to protect the locations of this rare species

Colony size in 2014 ranged from 0.3 m^2 to 21 m^2, while in 2018 colony size ranged from 0.3 m^2 to 105 m^2. Between both surveys *Physostegia correllii* was most commonly associated with herbaceous species such as *Ambrosia*., *Daucus*, and *Boehmeria* species. In both surveys about 40% of colonies were associated with non-native species. *Colocasia esculenta* was the most common non-native species associated with *P. correllii*, although *Iris pseudacorus*, *Arundo donax*, and *Alternanthera philoxeroides* were also noted.

Riparian canopy cover varied from no canopy cover to dense canopy cover, with *Taxodium distichum* and *Fraxinus pennsylvanica* being the most commonly associated riparian trees. Most colonies were found within light to moderate canopy cover. Soil tended to be silty sediment or organic detritus composed of broken down organic debris. Other soil types included gravel, bedrock, and sand. Two colonies were observed growing within cracked concrete.

Typically, *Physostegia correllii* colonies are composed of multiple stems united via an underground rhizome system. Colonies tend to grow parallel to the water's edge or along flat sediment banks with completely saturated soil. Plants rarely grow in the water but always grow in saturated soils in a "wet feet; dry ankle" situation.

Figure 3. Top. Two large *Physostegia correllii* colonies (indicated by black arrows) located in 2014. Bottom. In 2018 the colonies were missing presumably due to brush clearing along the bank.

Figure 4. A new colony location for 2018 that was not present during the 2014 survey. This colony was growing in saturated deposited sediment with no canopy cover, but associated with *Colocasia esculenta*

Table 1. Descriptive data for *Physostegia correllii* colonies.

	2014	2018
Colony Count	23	23 (8 colonies not relocated from 2014 survey but 8 new colonies were identified)
Colony stem count range	5 to 65	1 to 75
Soil type		
Organic/Detritus	20%	50%
Silt	60%	30%
Other	20%	20%
Riparian Cover		
None	8%	9%
Light	56%	45%
Medium	17%	27%
Dark	13%	18%
Associated species		
Native	57%	60%
Mixed Native/ non-native	43%	40%

Discussion

Physostegia correllii appears to be well established along the banks of Lady Bird Lake. Our surveys showed three distinct spots where colonies were aggregated in close proximity to one another. Six new colonies surveyed in 2018 were established along the northern edge of the lake where no colonies were observed four years prior. A few of these colonies may have been planted as part of habitat improvement projects along the Ann and Roy Butler trail, which is maintained by the non-profit Trail Foundation (Anna Strong, pers. comm.). Two new colonies were found on islands and were presumably naturally occuring. All new colonies were found growing on low lying sediment bars with less dense vegetation mostly dominated by quick-growing herbaceous species or very young *Salix* species. These sediment bars were likely deposited during the multiple significant flooding events that occurred at Lady Bird Lake since 2014. Conversely, the one colony located below Longhorn dam in the Colorado River was likely lost due to the same flooding events, as this area was completely scoured of all vegetation by 2018.

Based on our observations *Physostegia correllii* colonies at Lady Bird Lake seem to be somewhat site specific. Suitable habitat can be characterized by the following:

1. Saturated alluvial organic, silty soils.
2. Moderate canopy cover
3. Absent or sparse low growing associated vegetation

In our survey there was obvious differentiation in habitat between newer colonies and longer established colonies. The newest colonies were associated with sparse vegetation while older colonies were surrounded by more mature and denser vegetation and growing on more compacted soils. In several instances however, newer colonies, presumably planted or otherwise, were also becoming overshadowed by *Colocasia esculenta*.

Physostegia correllii health appears to decline in areas with dense riparian vegetation or canopy cover. Colonies that were located with dense riparian growth were notably less robust and exhibited leaf yellowing, insect damage, and decreased flower production. Some 2014 colonies in these growing situations were significantly reduced in size between the two surveys.

Physostegia correllii may be characterized as a stream edge specialist and disturbance fugitive that thrives on newly deposited sediment beds before more robust riparian and wetland vegetation takes hold. If this is the case, then the persistence of the species depends on the creation of new habitat or maintenance of existing habitat (scouring of dense riparian vegetation) by flooding events along streams and rivers. Dependence on fluvial disturbance is typical in riparian plant communities. Floodplain scouring and deposition of sediments creates new habitat (Bendix & Hupp 2000), can reduce non-native populations (Greet et al. 2015), and can increase biodiversity (Catford & Jansson 2014). Riparian plants such as *P. correllii* have several adaptive traits (i.e., rhizomes, flexible stems) that allow them to resist scouring and/or anoxic conditions associated with floods (Catford & Jansson 2014).

Management and conservation

Riparian areas in general are sites of high biodiversity because of their position at the transition zone between terrestrial and aquatic habitat, their role as linear connections among varied landscapes (Naiman et al. 1993), and their interactions with fluvial and geomorphic processes (Naiman & DéCamps 1997; Osterkamp & Hupp 2010). Changes in hydrologic processes as a result of dam operations can threaten riparian vegetation communities by altering moisture and sediment regimes (Poff et al. 1997) and impeding dispersal (Jansson et al. 2000). Because *Physostegia corellii* occurs along rivers that have multiple dams (i.e., Colorado River, Rio Grande), continued monitoring is necessary to conserve this rare species. In the present study, we observed that water levels in the Colorado River below Longhorn Dam vary widely throughout the day. More water is released from the dam at peak hours to meet hydropower needs, then the water level drops significantly in the evening as the demand for electricity decreases. The rapid changes in water levels and associated changes in soil moisture and sediment deposition may partially explain why we did not observe any populations near the Montopolis Bridge, where the species was known to occur in 1952. In contrast, still to slow-moving waters in Lady Bird Lake may somewhat benefit *P. correllii* by allowing deposition of fine sediments and organic debris after minor flood events. Lady Bird Lake is also a constant-level reservoir in which water levels fluctuate very little during operating times and average flows.

Noted threats to *Physostegia correllii* growing along Lady Bird Lake include stream bank erosion, competition from non-native species, and disturbances such as mowing, herbicide application, or construction in the riparian areas. *Physostegia correllii* would likely benefit from the control of *Colocasia esculenta* and other non-native species. Some non-native species are able to inhibit recruitment of associated natives by reducing the amount of light available to the soil surface (Maskell et al. 2006). *Colocasia esculenta* and *Arundo donax* grow in dense colonies and *P. correllii* seems sensitive to reduced light availability. Control of non-natives should be done with care, however, as *P. correllii* colonies do occur with colonies of non-natives (Figure 3). For example, three colonies located in 2014 were noted as extirpated due the removal of *Arundo donax*, general brush clearing, or mowing along the lake edges (Figure 4). Foot traffic along the stream edge can also have a negative impact on *P. correllii* when trampling compresses and hardens the substrate.

The ability for *Physostegia correllii* to reemerge after a period of disturbance or competition is unknown but possible if the rhizome mass stays viable and intact. Plants readily produce seed but no seedlings have been observed during our monitoring efforts. Viable fragments have been observed, including rooted stem fragments and broken rhizomes but it is not known which propagative method is most likely to produce the current colonies. Fragmentation is readily used as a colonization method in many aquatic and wetland plants, especially flood adapted species (Barrat-Segretain & Bornette 2000).

Although the Travis County populations of *Physostegia correllii* are located in a highly urbanized environment, restoration and/or protection of the riparian habitat is possible. Prevention of excessive mowing and trampling of the riverbank has been effective along urban streams in encouraging growth of native vegetation (Riley 2016). Though complete restoration of an urbanized and impounded riparian habitat to an unaltered state is not realistic (Wohl & Merritts 2007),

preservation of locations with extant *P. correllii* colonies is possible. Although *P. correllii* is occasionally planted along the Ann and Roy Butler Trail as part of beautification projects, further establishment into other sites along Lady Bird Lake and the implementation of an ecologically based conservation plan or refugium would be beneficial to this species.

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NEW VASCULAR PLANT RECORDS FOR KENTUCKY

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ABSTRACT

Twelve new species are documented for the flora of Kentucky, including eight native and four non-native taxa: *Anemone ranunculoides, Callicarpa americana, Dichanthelium annulum, Erigeron allisonii, Houstonia micrantha, Lamium galeobdolon, Lepidium oblongum, Poa wolfii, Rhynchospora gracilenta, Trillium stamineum, Viburnum dilatatum,* and *Vicia minutiflora.*

Twelve new species have been documented for the state of Kentucky over the course of the past five years of field work and herbarium study. The details of each species' discovery, along with specimen citations, are outlined below.

Of these species, eight were discovered from simple on-ground exploration of various locations across the state. The four others were discovered as part of a National Science Foundation grant received by Austin Peay State University (ASPC) to rescue and integrate the former Western Kentucky University (WKU) collection. The WKU herbarium had itself, just a few years before closing, received and integrated the Davies herbarium from the University of Louisville (DLH) and acquired the largely unprocessed private collection of Max Medley. The NSF grant is providing funding to verify identities of all incoming specimens before integration into APSC and to process the Medley collection. As a result of this funding, these additional three new species for Kentucky were discovered.

The flora of Kentucky remains poorly known compared to neighboring states, with relatively sparse county-by-county range documentation (Kartesz 2015). The earliest complete county-by-county mapping is from efforts less than a decade old (Campbell & Medley 2012). Due to this gap in floristic knowledge, I have made it a priority to increase Kentucky collections, particularly in the diverse but scarcely documented south-central portions of the state. It should be noted that the floristic knowledge of counties along the Tennessee border remains remarkably incomplete.

The following is a list of the new species for the state. Non-native species are marked by an asterisk (*).

***ANEMONE RANUNCULOIDES** L. [Ranunculaceae]

This European species was documented at a bridge crossing a tributary of the Licking River in Bourbon County. It was growing abundantly on rich, calcareous slopes among native spring wildflowers such as *Cardamine diphylla, Dicentra cucullaria, Stylophorum diphyllum, Stellaria corei,* and *Thalictrum dioicum*. This represents the first documented instance of naturalization within the USA. It has been present at this location since at least at least 2012, when it was initially photographed by myself (and misidentified as *Ranunculus hispidus*).

This population was on a steep slope, which would be atypical for any sort of ornamental cultivation but it perhaps is a location where dumping might occur. It is unclear what the invasive potential for this species is, because the slopes were not surveyed beyond the vicinity of the bridge crossing.

Voucher. **Kentucky**. Bourbon Co.: W of Colville Covered Bridge, on the S side of the crossing of Hinkston Creek (South Fork of the Licking River), N-facing, steep mesic calcareous slope forest, trashed but with surprisingly ample native vegetation, 38.32424° -84.20335°, 16 Apr 2017, *Brock 1654* (APSC).

CALLICARPA AMERICANA L. (L.) [Lamiaceae]

This southeastern shrub is documented for the first time as a Kentucky native, in the Land Between the Lakes in Lyon County. It is found growing on the thin calcareous woods above the bluffs of the Cumberland River, associated with *Ulmus serotina*. Only a single depauperate individual, less than 1 meter tall, was observed.

The discovery of *Callicarpa americana* this far north was unexpected, as it is apparently absent from the bluffs of the Cumberland River in more southern areas of the Land Between the Lakes. The closest known populations of this species are located along the Tennessee River in Humphreys Co., Tennessee, where it grows on calcareous slopes.

Initially, there was some question as to whether this individual really does indicate the existence of a native population of *Callicarpa americana*. However, the remoteness of the locality (with the topography being an impossible location for a homestead), the similarity to its typical habitat further south, and the difficulty of surveying steep bluffs, all point to this individual being native. This locality has not been revisited since the initial discovery, and it is likely that further surveys will reveal more individuals.

Voucher. **Kentucky.** Lyon Co.: W bluff of the Cumberland River, at the end of a ridge that extends E from just S of the terminus of Old Ferry Road, on the middle prong of the three ridges, dry calcareous bluff at the edge of the old Cumberland River, one small plant seen, N 37°01'41'' W 88 °04'29'', 31 Jul 2014, *Brock 589* (APSC).

DICHANTHELIUM ANNULUM (Ashe) LeBlond [Poaceae]

A specimen of *Dichanthelium annulum* from the Cumberland River bluffs in Pulaski County was found in the Medley collection. The specimen had only previously been identified to the genus *Dichanthelium*.

Dichanthelium annulum is a poorly known species and is considered rare across its entire range. Its typical habitat has been described as "dry rocky or sandy soil of open woods and calcareous grasslands (barrens)" (Leblond 2001). This is compatible with the habitat Medley described on his specimen, "open, cliff edge limestone glades," which is a community often referred to a "calcareous barren" in some classification schemes. Medley's specimen of *Dichanthelium annulum* is found on the same river bend as with another species that is restricted to a single known locality in the state, *Tragia urticifolia*, which is also found in this xeric limestone barren community.

Voucher. **Kentucky**. Pulaski Co.: Open, cliff edge limestone glades and adjacent woods on SW-facing cliffs of Cumberland River on Cox Bend, Burnside 7.5' Quad, 22 Jul 1987, *Medley 17465* (APSC).

ERIGERON ALLISONII Poindexter, Keener, & Noyes [Asteraceae]

This species was recently described (Weakley et al. 2018), elevating to species status the variety known as *Erigeron strigosus* var. *calcicola*.

While this species is common in limestone glades of the Nashville Basin, it has never before been documented in similar habitats in the Pennyroyal Plain. This was not entirely unexpected however, as the Pennyroyal Plain glades are comparatively depauperate and lacking many species

characteristic of the Nashville Basin glades (e.g. *Dalea gattingeri, Leavenworthia stylosa, Pediomelum subacaule*). It was then somewhat surprising to find a specimen of this taxon in the WKU collection, vouchered from a remnant glade at the edge of the city of Bowling Green. The collection was made in 1980 as part of a floristic study of a remnant glade complex on private land (Johnson 1981). The glade complex has apparently been substantially reduced in size since the 1981 study due to development.

This site was visited by myself and other botanists in July 2016, prior to being made aware of the existence of the *Erigeron allisonii* specimen. The remaining glade appears to remain in moderately intact condition, with the state-Threatened *Juncus filipendulus* being documented there from the first time in Warren County. However, the glade is located on private land in a rapidly urbanizing area and is under imminent threat of development. An unfinished road has been constructed that appears to be leading directly into one of the two remaining glade outcrops in this area. As of this publication, the location has not been revisited to determine whether *E. allisonii* is extant at this site.

Voucher. **Kentucky.** Warren Co.: Exposed limestone, 2.1 km NW of the intersection of Hwy 231 and US 68, with *Scutellaria* and *Sedum*, 5 Apr 1980, *Johnson 1242* (APSC)

HOUSTONIA MICRANTHA (Shinners) Terrell [Rubiaceae]

This species has been documented in Barren County, representing a significant range extension to the northeast of the nearest known locality. Populations were found in mowed areas near Mammoth Cave National Park, around roadsides, weedy lawns, and a cemetery. At the Diamond Caverns visitor's center, it is growing approximately 200 meters from the Edmonson County line.

In this vicinity, it appears to have a preference for dry, sandy soil with relatively sparse vegetation. In these areas it is sympatric with *Houstonia pusilla,* which is more common in the Mammoth Cave area and found in a wider range of habitats.

It is unknown if this population is the result of *Houstonia micrantha* extending its range northward in recent times or if this diminutive, ephemeral annual has been simply overlooked. Further searches in other sandy cemeteries in western Kentucky, such as Utley Cemetery in Marshall County, Edgewood Cemetery in Todd County, and Jenny Ridge Cemetery in Trigg County, failed to reveal any further populations. This suggests the population of *H. micrantha* at Mammoth Cave and Zion Cemetery may be somewhat isolated.

Voucher. **Kentucky.** Barren Co.: Zion Cemetery, NW of Park City, gravelly roadside just E of the cemetery, also seen by the parking lot on the E side of Mammoth Cave Parkway N of Doyle Road, abundant in areas of thin soil along roadside and gravelly, sandy trailside, corolla pure white, tube ~2 mm, 37.100353° -86.055544°, 2 Apr 2018, *Brock 1883* (APSC).

***LAMIUM GALEOBDOLON** (L.) Crantz [Lamiaceae]

This European species is documented in Kentucky along the Elk Fork (a tributary to the Red River) in Todd County and in both Cherokee and Iroquois parks in Louisville.

In Todd County, it was found along a gravel roadside in a young *Acer negundo*-dominated bottomland. Although this particular location is weedy, with much *Alliaria petiolata* and *Galium aparine*, just south of this vicinity is a location where the native *Trilium stamineum* was documented new for the state (see section below). The source of the *Lamium* population is unknown. It appears to be proliferating only locally along the highly disturbed forest edge.

Additional specimens from Jefferson County were located in the EKY herbarium, collected by Patricia Haragan. These were previously misidentified as *Lamium maculatum*, a species not known to escape in Kentucky. On the label she has indicated that plants at the Cherokee Park location have

established since 2005 and are "choking out other herbaceous species." *Lamium galeobdolon* is considered an invasive species in some areas of the USA and it should be considered a potential threat to Kentucky communities.

Vouchers. **Kentucky.** Jefferson Co.: Cherokee Park, in open woodland mid-slope, E-facing, along old trail, 19 Apr 2010, *Haragan s.n.* (EKY). Todd Co.: E side of the Elk Fork, at Old Watermelon Road low-water bridge crossing, edge of young bottomland forest along dirt roadside, 37.100353° -86.055544°, 20 Apr 2019, *Brock 2287* (APSC).

***LEPIDIUM OBLONGUM** Small [Brassicaceae]

This weedy mustard has been documented in Fayette and Todd counties. Both locations are in urban areas that receive frequent mowing, with thin soil due to asphalt or concrete.

This species was first brought to my attention by Dr. Julian Campbell in 2013, who collected a specimen from Lexington in a location he described as a "Nostoc and cigarette butts along a medium of a busy highway." Although Campbell initially identified the specimen as *Lepidium ruderale*, I annotated it to *Lepidium oblongum* upon further examination in 2016 (an identification he now concurs with). A second population was also discovered in 2019 along on old sidewalk edge in Guthrie, Todd County.

Although this species is native to the south-central USA, with populations documented from as close as Arkansas in the 1880s (*Letterman s.n.,* UARK), there is no evidence that *Lepidium oblongum* is native to Kentucky. The two localities are in maximally disturbed urban habitats, with no indications of the plants spreading beyond. Because of this, *L. oblongum* considered here as adventive in the state.

Vouchers. **Kentucky.** Fayette Co.: Abundant on medium along Tates Creek Road and New Circle Road, 17 Apr 2013, *Campbell s.n.* (APSC, EKY). Todd Co.: Guthrie, N side of Park Street (Hwy 41) on W side of town, rare at weedy unmowed edge of sidewalk though an old neighborhood, 17 Apr 2019, *Brock 2297* (APSC).

POA WOLFII Scribn. [Poaceae]

A specimen of *Poa wolfii* has been discovered in the Max Medley collection, from the bottoms of the Salt River in Bullitt County. Medley had previously identified the specimen only to genus level, as he did with many of his graminoid collections.

At the Bullitt County site, it is found in the broad bottoms of the Salt River as it winds through an area underlain by Devonian shale. This particular ecological community is poorly known in Kentucky, being located nearly entirely inside Fort Knox, a military installation. The *Poa wolfii* location is in the most upstream portion of this bottomland region, where a small portion of the community located outside Fort Knox in the vicinity of Shepherdsville. If this habitat could be explored further, more populations of *Poa wolfii* probably could be located.

The range of *Poa wolfii* is concentrated in the midwestern USA, where it is found in both bottomland and upland forests. At the Bullitt County site, Medley documented it growing sympatrically with *Poa sylvestris.* No attempt has been made to relocate the species in the field.

Voucher. **Kentucky.** Bullitt Co.: S side of Mud Run and W of Blue Lick Road, low flatwoods, 20 May 1988, *Medley 18946* (APSC).

RHYNCHOSPORA GRACILENTA A.Gray [Cyperaceae]

A specimen of *Rhynchospora gracilenta* has been discovered in the Max Medley collection, from the Cumberland Plateau in McCreary County. Medley had previously identified the specimen only to genus. The location is from an artificial pond on a ridgetop in what is now known as the Blue

Heron Campground. However, according to historic aerial photography, when the specimen was made in 1980 this site appears to be simply along an undeveloped dirt trail. The pond appears to still exist, although it has not been revisited to determine of *Rhynchospora gracilenta* is extant.

Rhynchospora gracilenta joins a few other species typical of open, acidic conditions that have their only Kentucky locality in McCreary County: *Parnassia asarifolia, Polygala polygama*, and *Sabatia brachiata*.

Voucher. **Kentucky.** McCreary Co.: Artificial pond, ridge top from Barthell to head of Natural Bridge Hollow, ca. 0.5 mi N of Natural Bridge on dirt trail, just N of old barn, 31 Jul 1980, *Medley 2711* (APSC).

Figure 1. *Trillium stamineum* in young upland woods, Logan Co., Kentucky.

TRILLIUM STAMINEUM Harbison [Trilliaceae]

This southeastern *Trillium* has been documented in Logan and Todd counties, which represent the northernmost known populations. The closest known localities are southward in Cheatham Co., Tennessee.

Trillium stamineum was found along Whipporwill Creek and the Elk Fork, both tributaries to the Red River. These populations are small, with around 50 total plants observed. At both sites, they are growing in calcareous forests the base of thinly forested bluffs, usually below exposed limestone cliffs. In addition, in the vicinity of Whipporwill Creek this species was also observed growing along the edges of steep sinkhole in a karst plain, with a few individuals even persisting in the grazed upland woods. These ecological integrity of these sites ranges from high quality, where it is associated with

spring ephemerals such as *Erythronium americanum,* to areas of heavy disturbance dominated by *Lonicera japonica*.

The southern portions of Logan and Todd counties lie in the Pennyroyal Plain ecoregion, a gently rolling karst landscape that was historically dominated by prairie vegetation, with the exception of areas protected from fire such as in river gorges and steep-sided sinkholes. The discovery of this species for the first time in the Pennyroyal Plain ecoregion was unexpected, as the ranges of many other taxa of calcareous habitats are at the edge of the Western Highland Rim in Tennessee and do not cross into the Pennyroyal Plain (e.g. *Nemophila aphylla*, *Rhododendron alabamense, Vicia minutiflora*). These calcareous slope forests of the Pennyroyal Plain in Kentucky in Trigg, Christian, Todd, Logan, and Simpson counties are generally poorly surveyed, due to lying entirely within privately owned land, with the exception of small city park in Simpson County. In the course of this exploration of Whipporwill Creek, 33 other new county records for Logan County were also vouchered.

Vouchers. **Kentucky.** Logan Co.: N of Dot, E side of Whippoorwill Creek at N end of bluffs that follow creek where the slope levels out, mesic slope with limestone exposure, thinly forested, with *Melica mutica* and *Lonicera japonica*, 36.70844° -86.96722°, 5 Apr 2016, *Brock 1234* (APSC). Todd Co.: E side of the Elk Fork, S of Old Watermelon Road low-water bridge crossing at first bend in the river, mesic calcareous forest, in lower areas of slope where it levels out, not in the steep N-facing bluffs, which are too thick with *Staphylea*, 25-50 plants, 36.66546°, -87.07528°, 20 Apr 2019, *Brock 2319* (APSC).

***VIBURNUM DILATATUM** Thunb. [Adoxaceae]

This non-native shrub was documented in the vicinity of Blue Heron, on the banks of the Big South Fork in McCreary County. It is spreading profusely, with young individuals in both disturbed and undisturbed mesic and riparian forest. In the USA, it is known almost exclusively from the New England and mid-Atlantic area, with sparse collections as far south as North Carolina (Weakley 2015). Its documentation in Kentucky represents a significant range extension westward.

Viburnum dilatatum is native to temperate forests of eastern Asia. From personal observation in the Kanto Region of Japan, it appears to thrive in openings in temperate forests and was the most common species of *Viburnum* that I encountered in that region.

The ability of *Viburnum dilatatum* to penetrate the forests of the Big South Fork, combined with bird dispersal, is alarming. It should be considered a high-level invasive threat in both Kentucky and Tennessee.

Voucher. **Kentucky.** McCreary Co.: Blue Heron, on the E side of the Big South Fork, abundant along the trails, parking lot edges, and other disturbed areas around this visitor's center, 36° 40‘ 05” N, 84° 32’ 48”W, 27 Sep 2014, *Brock 755* (APSC).

VICIA MINUTIFLORA F.Dietr. [Fabaceae]

This diminutive legume is documented here from Trigg County, discovered during an exploration of the southwest-facing bluffs of the Cumberland River at the state line. It is a species of the southeastern USA, typically found on calcareous bluffs and rocky limestone forests of the Interior Low Plateau, where it is common. It has previously been documented from three Tennessee counties bordering Kentucky (Kartesz 2015).

Vicia minutiflora is uncommon at this locality — with about 10 plants were observed. This community is a dry calcareous woodland with limestone outcrops, and the *V. minutiflora* was located above (but not on) the bluffs of the river. *Hypericum frondosum* was also documented as a new county record, occurring in abundance at this site.

Figure 2. *Vicia minutiflora* on the bluffs above the Cumberland River in Trigg Co., Kentucky.

A search of the APSU herbarium found no herbarium specimens collected from this area, which indicates little to no prior floristic work has been conducted at this site. However, Trigg County itself is relatively well floristically surveyed, since contains a portion of the Land Between the Lakes National Recreation area, which is located on the west side of the Cumberland River.

Voucher. **Kentucky.** Trigg Co.: E side of the Cumberland River, N of unnamed stream N of the state line, part of the "Linton Public Use Area," high limestone bluffs along edge of river, in vicinity of *Ulmus serotina* and *Hypericum frondosum*, 36.67234° -87.90474°, 27 Apr 2016, *Brock 1315* (APSC).

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NUEVOS REGISTROS DE PLANTAS VASCULARES PARA LA FLORA DEL ESTADO DE GUERRERO, MÉXICO. I.

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RESUMEN

Se presentan siete especies (pertenecientes a seis géneros) de plantas vasculares como registros nuevos para la flora del estado de Guerrero, México. En cada caso se presenta una descripción breve, se señalan los ejemplares de referencia y se menciona su distribución general.

ABSTRACT

Seven species (belonging to six genera) of vascular plants are presented as new records for the flora of the state of Guerrero, Mexico. In each case a brief description is presented, the voucher specimens are indicated, and the general distribution is noted.

En el estudio de la flora arbórea del estado de Guerrero se tiene un registro preliminar de 560 especies para la Cuenca del Río Balsas (Fernández et al. 1998), por ello no es difícil suponer que el estado alcance un total superior a las 1000 especies, cifra mayor a las registradas para los estados de Michoacán (845 especies), Colima (535), Quintana Roo (351), Campeche (297), Yucatán (287), y Sonora (285), de acuerdo a Cué-Bärr et al. (2006), pero posiblemente inferior a las 1140 especies de Jalisco, anotadas por Ramírez et al. (2010) en su inventario florístico estatal.

En la elaboración del estudio de la flora arbórea para el estado de Guerrero se hallaron especies, nunca antes registradas para la región. El caso de *Connarus stenophyllus* Standl. & Williams ex Molina es peculiar, pues siempre se le había tratado como un endemismo de Chiapas y en el presente trabajo se extiende su distribución hasta Oaxaca y Guerrero (Jiménez y Cruz 2014). Llama la atención el registro de *Vauquelinia australis* Standl. en la porción central del estado de Guerrero pues únicamente se le conoce de la Mixteca poblana y del Valle de Tehuacán (Jiménez et al. 2016); finalmente es muy interesante encontrar a *Ormosia carinata* Zamora, ya que solamente se había colectado en de la región de Uxpanapa en los estados de Veracruz y Oaxaca (Cruz & Jiménez 2015).

Sin embargo, para el estado de Guerrero se han localizado otras especies de plantas que no se registran en el estudio de Villaseñor (2016): Taxonomy and systematics Checklist of the native vascular plants of Mexico. Catálogo de las plantas vasculares nativas de México.

Así, se presentan siete especies, en seis géneros (*Brongniartia*, *Bouvardia*, *Lathyrus, Nama, Styphnolobium,* y *Weinmannia*) como nuevos registros para el estado. Es obvio, que la flora del Guerrero se ha enriquecido por elementos de muy diversos orígenes, algunos inesperados, gracias a la ubicación geográfica del estado y a la complejidad ambiental del mismo, sin embargo, cabe señalar que la incorporación de nuevos registros a la flora de Guerrero es un indicativo de que aún falta conocer mucho más para entender la riqueza de la flora en este estado mexicano.

1. BRONGNIARTIA PAPYRACEA O. Dorado & D. M. Arias. **Leguminosae**. Arbustos caducifolios de 4 a 5 m de alto, en selva baja caducifolia o selva mediana caducifolia, a 223–256 m de altitud. Tallos con corteza exfoliante café-rojiza, con abundantes lenticelas blancas. Inflorescencias en racimos terminales de hasta 18 cm de largo, el raquis es pubescente, con abundantes brácteas foliáceas, falcadas, 1.8–2.2 × 1–1.4 cm, pubescentes en el envés. Flores de 2 cm de largo, con pétalos morados, generalmente una por nudo, el pedicelo 1.5–2 cm de largo, pubescente, el cáliz 1.5 cm de largo, pubescente externamente, el estandarte es orbicular, 2 × 1.8 cm, el ala oblonga, 2 × 1.4, la quilla 1.7 × 0.7 cm, el androceo 2 cm de largo. Frutos inmaduros, 5–6 × 1.3–1.5 cm, con brácteas persistentes.

En el Municipio de Coahuayutla se le conoce como gallinillo. Según Dorado y Arias (2006) esta especie es endémica de Jalisco y suroeste de Michoacán, en la porción occidental de la Cuenca del Balsas.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. Coahuayutla: Coahuayutla, 1.5 km al SE, salida a Coahuayutla, 18°18´6.0”N, 101°43´27.9”O, 16 mayo 2011 (fruto), *Soto* y *Santacruz 18695* (FCME, MEXU); 11 km al SE, carretera La Unión–Coahuayutla, 18°14´15”N, 101°46´8.2”O, 15 mayo 2011 (flor y fruto jóvenes), *Soto* y *Santacruz 18691* (FCME, MEXU).

2. BRONGNIARTIA ALAMOSANA Rydb. **Leguminosae**. Árboles caducifolios, de 4.5 m de alto, en altitudes de 422 m, en selva baja caducifolia perturbada. Tallos ramificados desde los 1–2 m de altura, corteza café–grisácea, con líneas de lenticelas. Hojas 7–9(–10.5) cm de largo, con 11–15 folíolos (seríceas cuando jóvenes), pecíolos 1.5 cm de largo, pubescentes. Folíolos elípticos, 2.3–2.5 × 1.5–1.6 cm, base obtusa, ápice obtuso, mucronado, haz ligeramente piloso, envés ligeramente piloso, pubescencia más abundante en la vena media, pelos glandulares rojizos en la base del peciólulo; estípulas 2 × 0.4 mm, lanceoladas, foliáceas, envés piloso. Frutos 4.5–5 × 1.8 cm, oblongos, glabros, con ala vexilar de 1 mm de ancho.

Villaseñor (2016) indica que la especie es conocida de los estados de Chihuahua, Jalisco, Michoacán, Oaxaca, Sinaloa, y Sonora.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. Aratichanguio: 5 km al SE, camino Aratichanguio-El Timón. 18°26´30”N, 101°20´36.6”O, 19 jun 2011 (fruto), *Soto 18875–A, 18875–B, 18875–C* (FCME).

3. STYPHNOLOBIUM PROTANTHERUM M. Sousa & Rudd. **Leguminosae**. Árboles de 20 m de alto, con corteza obscura, en bosque de *Quercus*, a 1581 m de altitud. Hojas de 16 cm de largo, con 13 folíolos; los folíolos 4.3–5.2 × 1.8–2.6 cm, elípticos, la base obtusa, el margen ligeramente velutino, el ápice agudo, haz y envés pilosos; pecíolo y raquis tomentosos. Frutos 3.5–4(–6.5) × 2.4 cm, negros, glabros, con estípite 2–3 cm de largo, con 1–3 semillas; semillas negras 2.8 × 1.5 cm.

Sousa y Rudd (1993) señalan que esta especie está registrada solamente de la costa Jalisco, en la región de Chamela, en selvas medianas subperennifolias a subcaducifolias.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. San Miguel Totolapan: Puerto de Las Tunas, 2.5 km al S, camino a Coronilla, 17°56'40"N, 100°15'15"W, 28 may 2011 (fruto), *Soto 18797* (FCME, MEXU).

4. LATHYRUS PARVIFOLIUS S. Wats. **Leguminosae.** Hierbas decumbentes, glabras, en bosque de coníferas, a una altitud de 2630 m. Hojas de 10-14 cm de largo, con 8 folíolos, zarcillos 5-6 cm de largo, folíolos 3-2.5 × 0.9-1.5 cm, elípticos, base aguda, ápice agudo, mucronado; estípulas 1.6-2 cm de largo. Inflorescencias 7-10 cm de largo, axilares. Flores 1.3-1.5 cm de largo, lila con blanco, pedicelos 3 mm de largo.

Villaseñor (2016) registra esta especie para los estados de Aguascalientes, Chihuahua, Coahuila, Ciudad de México Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Tamaulipas, Veracruz, Zacatecas.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. Xalpatlahuac: Tototepec, 16 km al SO, camino que va de Tlapa a Marquelia, 2 jun 1981 (flor), *Lorea 1311* (FCME).

5. NAMA JAMAICENSIS L. **Hydropyllaceae**. Hierbas decumbentes, híspidas, la pubescencia blanca, hasta 40 cm de largo, en bosque tropical caducifolio, a 1250 m de altitud. Tallos híspidos, alados, el ala verde. Hojas 1.8–3 × 0.9–1.2 cm, subespatuladas, ápice obtuso, base decurrente, formando ala en el tallo. Flores axilares, solitarias, 8 mm de largo, corola blanca, lóbulos del cáliz 4 mm de largo, híspidos. Frutos cápsulas con tres líneas de dehiscencia, oblongas, glabras, 6 mm de largo, con cáliz acrescente hasta 10 mm de largo. Semillas esféricas, con testa reticulada.

Villaseñor (2016) señala que su distribución abarca los estados de Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Guanajuato, Hidalgo, Jalisco, Michoacán, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Yucatán, y Zacatecas.

Pérez (2013), para Flora de Guerrero, señala sólo la presencia de *Nama undulata* Kunth, *N. origanifolia* Kunth, y *N. dichotoma* (Ruiz & Pav.) Choisy.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. Eduardo Neri: Amatitlán, 0.3 km al O, 27 ene 1995 (flor, fruto), *Alejandre 18* (FCME, MEXU).

6. BOUVARDIA OBOVATA Kunth **Rubiaceae**. Hierbas erectas, 0.5 m de alto, en bosque de *Quercus*, a una altitud de 1780 m. Tallos cuadrangulares, glabros. Hojas en verticilos de 4, 8.5–9.5 × 2.3–3.2 cm, elípticas, glabras, sésiles; margen con pelos etrigosos, ápice y base agudos; estípulas tringulares, margen laciniado, rojizas. Inflorescencias cimosas, terminales, 6 a 7 cm de largo. Flores rojas, 2.5–3 cm de largo; lóbulos 3 mm de largo, interior del tubo de la corola sin anillo de pelos, estilo 2.5 cm de largo, glabro.

De acuerdo con Villaseñor (2016) se le localiza en Ciudad de México, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, y Tlaxcala. Sin embargo, Borhidi (2006) la registra sólo para la Ciudad de México y Morelos.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. Pedro Ascencio Alquisiras: Puerto Obscuro, 13.4 km al S, 18°31´42"N, 99°5159"W, 7 ago 1998 (flor), *Calónico* y *Jiménez 9573* (FCME).

7. WEINMANNIA INTERMEDIA Schltdl. & Cham. **Cunoniaceae**. Arbustos 3 m de alto, en bosque mesófilo de montaña, a una altitud de 2200 m. Ramillas velutinas, con pubescencia ferrugínea. Hojas 3.5– 6.5(–7.3) cm de largo, imparipinnadas, con (9–)11–15(–17) folíolos, folíolos 0.8–1.6(–2) × (0.4–)0.5–0.8(–0.9) cm, elípticos, los terminales romboides, margen con (5–)6–7(–8) dientes serrados por lado, base

decurrente, coriáceas; raquis alado, híspido en la parte abaxial, pubescente en el haz, el ala 1.5–2 mm de ancho, glabra; estípulas 6–7 mm de largo, 6 mm de ancho, ápice obtuso, lado externo piloso. Inflorescencias racimos axilares, 5–6.3(–7.2) cm de largo, pedúnculo 1.5–1.7 cm de largo, raquis piloso, pedicelos 1.8–2 mm de largo, pilosos. Flores pentámeras. Frutos2.5–3 mm de largo (sin considerar el estilo), 1.5–1.7 mm de ancho, ovoides, glabros, pardos 3–5 mm de largo.

Según Villaseñor (2016), a esta especie sólo se le ha reportado en los estados de Hidalgo, México, Oaxaca, Puebla, y Veracruz. Y de acuerdo a Morales (2010), solamente se ha registrado en los estados de Hidalgo, Oaxaca, Puebla, y Veracruz.

Ejemplares de referencia. **MÉXICO. Guerrero.** Mpio. Malinaltepec: Aproximadamente 3 km al SE de Paraje Montero, 4 may 1989 (flor, fruto), *Muñoz 220* (FCME, MEXU).

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PANICUM TYPES AT THE UNIVERSITY OF NORTH CAROLINA HERBARIUM (NCU)

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ABSTRACT

Examination of more than 4300 *Dichanthelium* and *Panicum* sensu lato specimens at NCU has resulted in the discovery of 35 additional type specimens, bringing the herbarium's total to 70, representing 46 names. Among them are several holotypes and lectotypes, and nine lectotypes had to be designated as a result of this investigation. Also discussed are specimens that were wrongly thought to be types, including those for invalid names. Detailed information is provided for each of the treated *Panicum* names, ihncluding protologue data, typification, and current treatment of the name.

A thorough examination has been made of the *Panicum* sensu lato collection at the University of North Carolina Herbarium (NCU). During that examination, completed in 2014, 35 type specimens not previously known to be in the collection were identified. That brings the herbarium's total of *Panicum* sensu lato type specimens to 70, representing 46 names (Table 1). Among them are 12 holotypes, 5 lectotypes, 17 isotypes, and 15 isolectotypes, making NCU a significant repository of *Panicum* types. It was also determined during this examination that nine *Panicum* sensu lato names were in need of lectotypification and this was accomplished in a separate paper (LeBlond 2015). All of those specimens are treated here, and portions of the introduction in that paper are repeated due to their essential application.

Type specimen determination required searches of older literature and online databases, and examination of type specimens in other herbaria. The Missouri Botanical Garden's Tropicos database (Tropicos 2018) provided the basis for nomenclatorial authority and type specimen documentation. Biodiversity Heritage Library (BHL 2018) provided access to several of the nomenclatorial protologues published during a particularly active period of *Panicum* field work and taxonomy in the late 19th and early 20th centuries.

There is a concentration of *Panicum* nomenclatorial literature from the work of George Vasey (1889) to the monumental treatment by A.S. Hitchcock and Agnes Chase in 1910. Hitchcock & Chase (1910) has often been cited for its remarkably comprehensive and coherent treatment of the massive *Panicum* complex. But it is also remarkable for its use of the type concept, which had only been codified three years before (Nomenclatural Commission 1907). Hitchcock & Chase attempted to locate and verify a type specimen for every name, including synonyms, in their 1910 treatment. This effort formed a significant part of the publication and was one of the earliest uses — if not the starting point — of a process now called lectotypification.

Identification of types in that era was complicated not only by the lack of consistent historical application but also by the nonstandardized documentation of collection data and specimen labeling. Specimen and/or sheet numbering by collectors was particularly troubling. Hitchcock & Chase noted that "It not infrequently occurs that two or more species, collected at the same time and place, or collected at different times and places but supposed by the collector to be the same species, are distributed under the same number to different herbaria." Dates of collection were also nonstandarized. Some collectors — including W.W. Ashe, G.V. Nash, and J.K. Small — used the inclusive dates of the field expedition as the date on the label. For example, Ashe indicated "June 10 – July 6, 1898" as the dates for an expedition that included the type collections of *Panicum glabrissimum* Ashe, *P. lucidum* Ashe, *P. mattamuskeetense* Ashe, and *P. roanokense* Ashe. Sometimes he recorded the month of collection without noting the year, indicating the date was only important phenologically.

During this era many new names were created, far more than are currently recognized. This was due in part to the disparity between those who worked in the field and those who worked in the herbarium. It was common for field botanists to have limited or no access to herbaria and botanical libraries. "On the other hand," wrote Gleason (1952), "the professional botanists [in the herbarium] often had little field experience with the plants which they studied. Careful study of plants in this country by competent men both in the field and in the herbarium is scarcely more than 50 years old."

The typification of 50 *Panicum* sensu lato names is treated here, 46 of which have one or more type specimens at NCU. The other four treated names are *P. amarulum* Hitchc. & Chase, *P. chrysopsidifolium* Nash, *P. eatonii* Nash, and *P. microphyllum* Ashe. The latter two names are represented by specimens at NCU that were thought to be types but which were determined not to be (Table 2). *Panicum amarulum* and *P. chrysopsidifolium* are included because of needed clarification of typification (Table 3).

Ashe authored 29 of the names treated here. He was the most prolific *Panicum* author, naming 48 entities altogether. Nash authored 13 of the names included here, second only to Ashe. Hitchcock & Chase authored two, and one each was authored by M.L. Fernald, F.L. Scribner, Scribner & Merrill, H.K. Svenson, and Vasey. Ashe's herbarium was donated to NCU in 1932, accounting for the large number of both Ashe and Nash types. It appears to have been a common practice for field workers in that era to exchange specimens for new names.

Five other NCU specimens regarded as types (representing four names) were rejected because the names are invalid (Table 2). Four specimens belong to three Scribner names that were never published — *P. biloxi, P. caricifolium* (two specimens), and *P. nitidum* var. *pubescens* — and one for an Ashe name that was published without designation of a type collection (*P. iowense*) and for which there are no known specimens. All of these names and so-called types are discussed at the end of the treatment under "Voucher Specimens for Invalid Names." Also briefly discussed at the end is the replacement name *Panicum halophilum* Nash and the status of specimens treated by some as its types.

The format begins with the currently accepted form of the name and its publication details, plus any other spelling forms of the specific epithet and where they appeared. This is followed by the typification data in the protologue, determination of type specimens by Hitchcock and Chase, the

classification and location of all known type specimens, classification commentary where needed (in all but three instances), Hitchcock and Chase taxonomic treatment, and current taxonomic treatment in Freckmann and Lelong (2003) and LeBlond (2019a, 2019b, 2019c).

Protologue typification. This includes all data provided by the nomenclatorial author relating to type collections, including locale, date, habitat, collector, and habit. When examining older *Panicum* types, it is important to go to the protologue. The author often cited additional collections that represented his or her concept of the named entity — what today are classified as paratypes and syntypes. Hitchcock and Chase frequently omitted references to additional collections in the protologue. Their concern was with the establishment of a primary type, either holotype or lectotype, along with verification of other specimens from the same collection. If more than one collection was referenced in the protologue, they chose the first mentioned as the primary type collection, following the newly published code.

Type specimen determination by Hitchcock & Chase. Because of the newness of the typification requirement, most elligible type specimens lacked a designation as type on the sheet itself, requiring deductive investigation. Hitchcock and Chase detailed their investigative procedure in the 1910 introdution: "Not infrequently the description [protologue] is based upon a single specimen, in which case there is no doubt as to what specimen is the type. Sometimes the author had several specimens at hand, in which case it becomes necessary to determine, if possible, which specimen represented to the author his ideal of the species. This may be shown, in case the author has designated no type, by the specific name, which may indicate a collector or locality, or by a careful comparison of the description, and especially of notes, with the specimens, or by some note upon the sheets of specimens which the author is known to have had before him at the time of describing the species. In the absence of any indication that will point toward a particular specimen, the first one mentioned or the one from the locality first mentioned with the original description, or at least the first one among those equally eligible, is chosen as the type." Hitchcock and Chase also provided a description of the habit of the specimen they recognized or designated as the type, a useful feature for subsequent investigations.

Unlike Ashe and other field workers, Nash did annotate the great majority of his holotype specimens by hand. Frequently, especially in the case of Ashe, Hitchcock and Chase could not locate the type specimen referred to in the protologue. A portion of the Ashe herbarium had been sent to the National Herbarium (US) in 1905, and another portion in 1908, but "Certain of Mr. Ashe's type specimens were not included in either of those loans." Many Ashe specimens for new names were unmounted in folders ("covers") or sometimes with both mounted and unmounted specimens in the same folder. Almost all Ashe type specimens were identified and designated as types anonymously by Chase (her handwritting is distinctive). She frequently referred to notes entered by Ashe on the folders, or on the sheets, or within the sheets, that helped in identifying the type specimen.

Hitchcock and Chase used the term "type" equally in regard to specimens designated by the author (holotypes) and those designated by themselves (lectotypes), and it is frequently difficult to determine whether a specimen they identified as a type is a holotype or lectotype. They often used "chosen" to indicate what now is called lectotypification of a specimen. They more frequently used the term "taken," but ambiguously, sometimes in the designation of an apparent (though not doubtless) holotype, and sometimes as lectotypification. There are instances where the "taken"

specimen appears to have been the only specimen found that represented the type but without designation as such by the author. Sometimes "taken" is used in their 1910 treatment to denote lectotypification of the first specimen listed of two or more specimens or sites in the protologue. There are at least two instances, *Panicum taxodiorum* Ashe and *P. wilmingtonense* Ashe, where Chase's reference to "taken as type" appears to refer to the entire contents of a folder in the author's herbarium, unmounted as well as mounted material. Ambiguous typification applies mostly to the Ashe specimens.

Types. All known holotype/isotype and lectotype/isolectotype specimens are listed for the treated names, with herbarium and specimen identification number provided for each specimen. The herbarium specimen number is usually the accession or catalogue number (e.g., NCU, US); the barcode number is used when it is the only identifying number (e.g., NY). The holotype/lectotype designator (when known) and location of designation are provided; designation was usually accomplished by annotation on the specimen sheet or by publication. Label data from the holotype/lectotype is also provided. A slash (/) with a space on either side is used to indicate breaks in the label data where needed for clarity. Collector names are not italicized unless that is how they are represented on the label.

In addition to the holotype/isotypes and lectotype/isolectotypes, all known syntypes, paratypes/paralectotypes, and topotypes/topolectotypes located at NCU are listed. Although not formally recognized by the International Code of Nomenclature (2012), topotypes/topolectotypes are frequently used in taxonomic literature. They deserve formal recognition, as they are almost always likely to be more closely related genetically to holotypes and lectotypes, and to their isotypes and isolectotypes, than are syntypes and paratypes, which were collected at other sites.

Commentary. This section primarily deals with how the type specimens were determined (the majority by Hitchcock and Chase) and how they were treated by subsequent workers (including me).

Taxonomic treatment by Hitchcock & Chase (1910). The taxon to which the name was assigned. Sometimes it was to the name as published in the protologue, but more often it was assigned in synonymy to another name.

Current treatment. The taxon to which the name is assigned in and Freckmann and Lelong (2003) and LeBlond (2019a, 2019b, 2019c).

TYPE SPECIMEN DETERMINATIONS

1. PANICUM ALABAMENSE Ashe, North Carolina Agric. Res. Serv., Bull. 175: 116. 1900, nom. illeg. hom., not Trin., 1854.

Protologue typification: "Auburn, Ala., May 7, 1898. Number 1530, Alabama Biological Survey" (Ashe 1900b, p. 116).

Type specimen determination by Hitchcock & Chase (1910, p. 244): "The type, in Ashe's herbarium, is a tuft of young vernal culms, the panicles only partly exserted. Mounted on the sheet with this is a specimen of *P. lucidum*. Ashe's description refers to the latter only in so far as the spikelets are said to be glabrous."

Types: **HOLOTYPE**: NCU 366. **ISOTYPES**: NY 381575; US 2383597 (fragm. ex NCU 366). Holotype designation: NCU 366 annotated as "type" by Chase, and published in Hitchcock & Chase (1910). Label data: "1530 / Alabama Biological Survey / *Panicum* / Auburn, Lee Co. / 5/7 1898 / F.S. Earle & C.F. Baker."

Commentary: The NCU specimen was annotated as "taken for type" by Chase. It apparently was the only specimen of type material found in Ashe's herbarium. On isotype US 2383597 is a single mounted fertile culm, and material in a packet. A Chase note reads: "from mounted specimen taken as type of *P. alabamense* Ashe." Both fragments are presumed to be from the holotype. Isotype NY 381575 was purchased from the Earle Herbarium in 1902 and appears not to have been seen by Hitchcock & Chase. It is annotated on the label as coming from the "type collection," and was also noted as an isotype by Gould & Clark in 1977.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum wilmingtonense* Ashe.

Current treatment: *Panicum wilmingtonense* is a synonym of *Dichanthelium ovale* (Ell.) Gould & C.A. Clark var. *addisonii* (Nash) Gould & C.A. Clark (LeBlond 2019a), and of *D. ovale* subsp. *pseudopubescens* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

2. PANICUM ALBEMARLENSE Ashe, J. Elisha Mitchell Sci. Soc. 16: 84. 1900.

Protologue typification: "in well drained open woods in Beaufort and Hyde counties, N.C., where the type material was collected by me May 26, 1899, near Scranton" (Ashe 1900a, p. 84).

Type specimen determination by Hitchcock & Chase (1910, p. 212): "The type specimen has been arbitrarily chosen from unmounted material in Ashe's herbarium in a cover marked on the outside '*P. albermarlense*,' and on a sheet upon which is written '*Panicum* ? very common in N.E. Beaufort County, also in Hyde, in open woods well drained.' There is nothing to indicate in which place the specimens were collected, except the published statement cited above."

Types: **LECTOTYPE**: US 2383612. **SYNTYPE**: NCU 17484. Lectotype designation: US 2383612 annotated by Chase "from material taken as type." Label data: see Commentary.

Commentary: US 2383612, the specimen designated as the lectotype, was prepared at the National Herbarium "from unmounted material in cover marked '*P. albemarlense*'." The location, date, and collection data are from the protologue. NCU 17484 includes a handwritten note by Chase: "type ? of / *P. albemarlense* Ashe / data agrees with that published, but no date of collection is given." There is no label or other Ashe data on the sheet. There are other instances where Chase's use of "type" refers to all material in a folder ("cover"), mounted and/or unmounted.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum albemarlense*.

Current treatment: *Panicum albemarlense* is a synomym of *Dichanthelium meridionale* (Ashe) Freckmann (LeBlond 2019a) and of *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *implicatum* (Scribner) Freckmann & Lelong (Freckmann & Lelong 2003).

3. PANICUM AMARULUM A.S. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 96. 1910.

Protologue and typification, from Hitchcock & Chase (1910, p. 96): "Type U.S. National Herbarium no. 592748, collected September 24, 1900, Virginia Beach, Va., by T.A. Williams (no. 3090)."

Types: **HOLOTYPE**: US 592748. **PARATYPE**: MO 2974815. Holotype designated by Hitchcock & Chase (1910, p. 96). Label data: "UNITED STATES DEPARTMENT OF

AGRICULTURE / North American Grasses Distributed by the Division of Agrostology / *Panicum amarum* Ell. / Virginia Beach, Va. / Sept 24th 1900 / No. 3090 / T.A. Williams."

Commentary: The MO 2974815 paratype specimen, Tracy 6508, was determined by me to be closer to *Panicum amarum* var. *amarum*, and was so annotated on 13 Jun 2012. The other many collections referenced in the protologue are also paratypes, but no attempt was made during this investigation to locate them.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum amarulum*.

Current treatment: *Panicum amarulum* is the basionym of *Panicum amarum* Elliott var. *amarulum* (A.S. Hitchcock & Chase) P.G. Palmer (LeBlond 2019a), and of *Panicum amarum* subsp. *amarulum* (A.S. Hitchcock & Chase) Freckmann & Lelong (Freckmann & Lelong 2003).

4. PANICUM ARENICOLA Ashe, J. Elisha Mitchell Sci. Soc. 15: 56. 1898. (Name spelled *P. arenicolum* in protologue, and *P. arenaecolum* on some Ashe sheets.)

Protologue typification: "Type material collected by the writer at Chapel Hill, N.C. June 1898, and later at several localities in the eastern portion of the same state" (Ashe 1898, p. 56).

Type specimen determination by Hitchcock & Chase (1910, p. 166): "The type could not be found in Ashe's herbarium. In Hitchcock's herbarium is a specimen labeled '*Panicum arenaecolum* Ashe' collected in the vicinity of Chapel Hill, North Carolina, by W.W. Ashe, and sent by him to Professor Scribner. The date of collection is not given. This specimen, which is probably a duplicate type, consists of two vernal culms, somewhat appressed-pubescent below; the stiffly ascending blades are glabrous except the lowermost, which is sparsely pubescent beneath."

Types: **LECTOTYPE**: NCU 20397. **ISOLECTOTYPES**: MO 1837598; NY 381579, 381580. Lectotype designation: NCU 20397 annotated and published by LeBlond (2015). Label data: "PLANTS OF THE SOUTHERN UNITED STATES IN THE VICINITY OF CHAPEL HILL, NORTH CAROLINA / *P. arenaecolum* Ashe / June / W.W. Ashe, Collector."

Commentary: Subsequent workers identified the type specimens at MO and NY as isotypes, apparently based on the then-missing type in Ashe's herbarium. Gould & Clark (1978) included the following in synonymy with *Dichanthelium aciculare* Desvaux ex Poiret: "*P. arenicolum* Ashe, 1898. Lectotype, US; isolectotypes, NY." There are no known types for this name at US, so the "Lectotype, US" must refer to the specimen from "Hitchcock's herbarium." However, the location of that specimen is unknown. Hitchcock & Chase's usual designation of a lectotype was with the phrase "chosen [or ambiguously, taken] as the type." Its absence here, plus the doubt in the term "probably," argue that Hitchcock & Chase did not select this specimen as the (lecto)type. In any case, since the location of the Hitchcock herbarium specimen is unknown, another specimen has to be chosen as the lectotype.

A specimen from the Ashe herbarium matching the protologue was found at NCU (no. 20397) during the current examination. It could well be the missing holotype, but lacks a type designation by Ashe on the sheet. It is selected as the lectotype.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum aciculare* Desvaux ex Poiret.

Current treatment: *Panicum aciculare* is the basionym of *Dichanthelium aciculare* (Desv. ex Poir.) Gould & C.A. Clark (Freckmann & Lelong 2003; LeBlond 2019a).

5. PANICUM AUBURNE Ashe, North Carolina Agric. Res. Serv., Bull. 175: 115. 1900.

Protologue typification: "Collected by Professors F.S. Earle and C. Baker, of the Alabama Biological Survey, at Auburn, Ala., May 7, 1898. No. 1527" (Ashe 1900b, p. 116).

Type specimen determination by Hitchcock & Chase (1910, p. 223): "The type specimen, in Ashe's herbarium, consists of several immature vernal culms with portions of the dead autumnal culms of the previous year attached."

Types: **HOLOTYPE**: NCU 17430. **ISOTYPES**: NY 381586; US 2383621 (fragm. ex NCU 17430). **SYNTYPE**: NY 381587. Holotype designation: NCU 17430 annotated as "type" by Chase. Label data: "1527 / Alabama Biological Survey. *Panicum* / Auburn, Lee Co. / 5/7 1898 / Coll. F.S. Earle, C.F. Baker."

Commentary: Syntype NY 381587 is assignable to *Dichanthelium sphaerocarpon* (Elliott) Gould. Since *Panicum auburne* is a synonym of *D. acuminatum* (Swartz) Gould & C.A. Clark, NY 381587 is therefore a syntype rather than an isotype.

Taxonomic treatment by Hitchcock & Chase (1910, p. 223): *Panicum auburne*.

Current treatment: *Panicum auburne* is a synonym of *Dichanthelium acuminatum* (Swartz) Gould & C.A. Clark var. *acuminatum* (LeBlond 2019a), and of *D. acuminatum* subsp. *acuminatum* (Freckmann & Lelong 2003).

6. PANICUM CHRYSOPSIDIFOLIUM Nash in Small, Fl. S.E. U.S. 100, 1327. 1903.

Protologue typification: "In dry sandy soil, middle Florida. Spring" (Nash 1903, p. 100). "Type, *Curtiss*, N. Am. Pl., no. D, in Herb. N.Y.B.G." (Nash 1903, p. 1327).

Type specimen determination by Hitchcock & Chase (1910, p. 168): "The type, in the herbarium of the New York Botanical Garden, is labeled 'Hammock land, Leon Co., Fla., May 12, 1886,' and consists of a clump of four vernal culms 30 to 55 cm. high with mature, short-exserted panicles."

Types: **HOLOTYPE**: NY 413960. **ISOTYPE**: US 2808891. Holotype designation: NY 413960 annotated as "Type" by Nash. Label data: "Curtiss. NORTH AMERICAN PLANTS. No. D / *Panicum chrysopsidifolium* / Lake Jackson, Leon Co. Fla. / Legit A.H.C. / May 12 '86."

Commentary: Hitchcock & Chase's statement that "the type" at NY is from "Hammock land, Leon Co. Fla.," differs from the NY 413960 label, which reads "Lake Jackson," also in Lake Co. The label on US 2808891 does read "Hammock land, Leon Co. Fla." with a Chase note stating "an excellent match for the type." This indicates she saw the specimen at NY that Nash had annotated as the (holo)type, so the difference in locality given for the NY specimen is likely a transcription error by Hitchcock & Chase. Because of the habitat difference indicated by "Hammock land" and "Lake Jackson," the NY and US specimens were likely collected at different sites, and I have concluded that US 2808891 should be treated as a paratype rather than an isotype.

In the protologue, Nash (1903, p. 100) describes the location as "In dry sandy soil, middle Florida," which seems to add to the confusion. But in that era, "middle Florida" referred to the panhandle region between Apalachicola River and Suwannee River. Labeling inconsistentcies were common in that era.

Treatment by Hitchcock & Chase (1910): *Panicum chrysopsidifolium*.

Current treatment: *Panicum chrysopsidifolium* is a synonym of *Dichanthelium filiramum* (Ashe) LeBlond (LeBlond 2019a). It is not treated by Freckmann & Lelong (2003).

7. PANICUM CILIOSUM Nash, Bull. Torrey Bot. Club 26: 568. 1899.

Protologue typification: "Type collected by S.M. Tracy, at Biloxi, Mississippi, September 1, 1898, no. 4580. . . . The specimen . . . is the late state and has the panicle included." (Nash 1899, p. 569).

Type specimen determination by Hitchcock & Chase (1910, p. 221): "The type, in Nash's herbarium, is the early autumnal form with a simple culm and primary panicle attached, and without the winter rosette. The specimen of *Tracy* 4580 in the National Herbarium has a winter rosette, the blades 4 to 6 cm. long. In the description the ligule is said to be 'about 0.5 mm. long' but in the type it measures 3 mm. long."

Types: **HOLOTYPE**: NY 413963. **ISOTYPES**: NCU 17360; US 2383619. Holotype designation: NY 413963 annotated as "Type" by Nash. Label data: "HERB. S.M. TRACY. 4580 / *Panicum ciliosum* Nash, sp. nov. ["*ciliatilaminum* Nash" crossed out] / HAB. Biloxi, Miss. Coll. S.M. Tracy 9/1 1898."

Commentary: None required.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum lanuginosum* Elliott.

Current treatment: *Panicum lanuginosum* is a synonym of *Dichanthelium acuminatum* (Swartz) Gould & C.A. Clark var. *acuminatum* (LeBlond 2019a), and of *D. acuminatum* subsp. *acuminatum* (Freckmann & Lelong 2003).

8. PANICUM COLUMBIANUM Scribner, Bull. Div. Agrostol., U.S.D.A. 7: 78, f. 60. 1897.

Protologue typification: "Dry, sandy fields, meadows, and open woodlands, New England southward to the Carolinas, and westward to Tennessee and Alabama, mostly near the coast; also in California. June-August" (Scribner 1897, p. 78).

Type specimen determination by Hitchcock & Chase (1910, p. 247): "The type ... is in Hitchcock's herbarium. It is labeled as follows in Scribner's writing: '*Panicum columbianum* Scrib. (Type) Brookland, D.C., July 14, 1894. Coll. F.L.-S.' The specimen consists of three branching culms, 25 to 38 cm. high, the primary panicles destitute of spikelets. A duplicate type is in the National Herbarium."

Types: **HOLOTYPE**: US 743463. **ISOTYPE**: NY 413965. **SYNTYPE**: NCU 17320. Holotype designation: US 743463 annotated as "Type" by Scribner. Label data: "*Panicum columbianum* Scribn. (Type) / *Panicum nitidum* Lam. var. *brevifolium* / Brookland, D.C. / July 14, 1894, Coll. F. L.-S."

Commentary: The label of NCU 17320 was prepared by the Division of Agrostology in Washington, D.C., and identifies it as "*P. columbianum* – Scribner. from type," without locality or date. The material consists of five culms with terminal panicles at anthesis and no axillary branching. Both the holotype at US and isotype at NY are in the primary phase of axillary branching, with terminal panicles that have shed their spikelets. This suggests the plants on the NCU specimen were collected at an earlier date or at a more northerly location. Since "from type" on the specimen sheet does not appear to refer to the holotype or isotype, it is presumed to refer to the group of specimens Scribner studied, and is here regarded as a syntype.

The location of the "duplicate type in the National Herbarium" is unknown. If found, it would be an isotype.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum columbianum*.

Current treatment: *Panicum columbianum* is the basionym of *Dichanthelium columbianum* (Scribner) Freckmann (LeBlond 2019a), and of *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *columbianum* (Scribner) Freckmann & Lelong (Freckmann & Lelong 2003).

9. PANICUM COMMELINIFOLIUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 29. 1898, nom. illeg. hom., not Rudge 1805. (Name spelled *P. commelinaefolium* in protologue and in Hitchcock & Chase 1910.) This nom. illeg. was later replaced by *P. curranii* Ashe, J. Elisha Mitchell Sci. Soc. 15: 113. 1899.

Protologue typification: "Based on material collected by Dr. J.K. Small near Stone Mt., Ga., Aug. 1-6, 1895, and distributed as *P. commutatum*" (Ashe 1898, p. 29).

Type specimen determination by Hitchcock & Chase (1910, p. 304): "The type, in the Biltmore Herbarium, consists of several late vernal culms beginning to branch, with short internodes and short-exserted panicles. The culms, sheaths, and both surfaces of the blades are puberulent, the blades 1.7 to 2.5 cm. wide, the spikelets 2.8 mm. long."

Types: **LECTOTYPE**: US 80590 (fragm., photo of holotype). **ISOLECTOTYPES**: NCU 17318; NY 413967; US 2478905, 2478926. Lectotype designation: US 80590 designated and published by LeBlond (2015). Lectotype label data (on packet of fragment from holotype): "*Panicum commelinaefolium* Ashe / Stone Mountain Ga. / coll John K Small, Aug 1-6, 1895 / (from Biltmore Herb)."

Commentary: The location of the holotype ("type") seen by Hitchock & Chase is currently unknown. The lectotype, formerly treated as an isotype, contains only a small fragment of material, but it is from the missing holotype, along with the photo.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum commutatum* Schultes.

Current treatment: *Panicum commutatum* is the basionym of *Dichanthelium commutatum* (Schultes) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

----------species name and 'type" as lower case caps, from here to the end (as in 1-9)

10. PANICUM COMMONSIANUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 55. 1898.

Protologue typification: "Based on No. 341, Commons. Collected in drifting sands along the coast, Cape May, N.J. June, 1898" (Ashe 1898, p. 55).

Type specimen determination by Hitchcock & Chase (1910, p. 242): "The type, in Ashe's herbarium, 'Ex. Herb. A. Commons,' consists of five tufts of vernal culms with mature primary panicles."

Types: **HOLOTYPE**: NCU 17314. **ISOTYPES**: NCU 17316; NY 413968; US 2383640. Holotype designation: NCU 17314 annotated as "n. sp." by Ashe, and published as "The type" by Hitchcock & Chase (1910). Label data: "HERB. A. COMMONS / *Panicum commonsianum*, W.W. Ashe n. sp. / drifting sands along the coast. Cape May. New Jersey. June 29, 1898. Coll. A.C."

Commentary: All four type specimens show June 29, 1898 as the date. Only US 2383640 indicates on the label that the collection number is 341, and that was entered by someone other than Ashe. The two specimens at NCU are from Ashe's herbarium. NCU 17314 is noted "n. sp." in Ashe's handwriting, while NCU 17316 is not. The former is the apparent holotype.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum commonsianum*.

Current treatment: Synonym of *Dichanthelium ovale* (Elliott) Gould & C.A. Clark var. *addisonii* (Nash) Gould & C.A. Clark (LeBlond 2019a), and of *D. ovale* subsp. *pseudopubescens* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

11. PANICUM CRYPTANTHUM Ashe, North Carolina Agric. Res. Serv., Bull. 175: 115. 1900.

Protologue typification: "Collected by writer in swamps at Wilson's Mill, N.C., in July, 1897" (Ashe 1900b, p. 115).

Type specimen determination by Hitchcock & Chase (1910, p. 299): "The type, in Ashe's herbarium, is a specimen arbitrarily chosen from among four bearing the label, 'Wilson's Mill, N.C. July 15, 1897. W.W. Ashe collector,' and with the additional data, 'In a small swamp on north side of railroad about one mile west of the station.' The name does not appear upon any of these sheets, but these plants agree with the description and are from the locality published. These specimens all are the autumnal form, with the reduced panicles partially included in the sheaths."

Types: **LECTOTYPE**: NCU 17544. **ISOLECTOTYPES**: NCU 17545, 17546; US 80522 (incl. fragm. ex NCU 17544). Lectotype designation: NCU 17544 "arbitrarily chosen" and published by Hitchcock & Chase (1910). Label data: "PLANTS OF THE SOUTHERN UNITED STATES / Wilsons Mill, N.C. / In a small swamp on North side of railroad about one mile west of the station. July 15, 1897, W.W. Ashe Collector."

Commentary: US 80522 contains a fragment of the lectotype in addition to the specimen Ashe mounted on it. Thus it contains two isolectotypes.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum cryptanthum*.

Current treatment: *Panicum cryptanthum* is the basionym of *Dichanthelium cryptanthum* (Ashe) LeBlond (LeBlond 2019a), and synonym of *D. scabriusculum* (Elliott) Gould & C.A. Clark (Freckmann & Lelong 2003).

12. PANICUM CURTIFOLIUM Nash, Bull. Torrey Bot. Club 26: 569-570. 1899.

Protologue typification: "Collected by S.M. Tracy at Ocean Springs, Mississippi, May 2, 1898, no. 4598" (Nash 1899, p. 570).

Type specimen determination by Hitchcock & Chase (1910, p. 267): "The type, in Nash's herbarium, consists of a tuft with two slender vernal culms about 30 cm. long, beginning to branch at the middle nodes. The blades are glabrous above except at the base and glabrous or sparsely pubescent beneath. In a duplicate type in the National Herbarium several blades have a few scattered hairs on the upper surface."

Types: **HOLOTYPE**: NY 413971. **ISOTYPES**: NCU 18039; US 340855, 743484. Holotype designation: NY 413971 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data: "Type. HERB. S.M. TRACY. 4598 / *Panicum curtifolium* Nash, sp. nov. ["*sphagnicolum* Nash" crossed out] / Hab. Ocean Springs Miss., COLL. S.M. TRACY. 5/2 1898."

Commentary: NCU isotype 18039 was in Ashe's herbarium, no doubt sent to him by Nash.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum curtifolium*.

Current treatment: *Panicum curtifolium* is the basionym of *Dichanthelium curtifolium* (Nash) LeBlond (LeBlond 2019a), and of *D. ensifolium* (Baldwin ex Elliott) Gould subsp. *curtifolium* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

13. PANICUM CUTHBERTII Ashe, J. Elisha Mitchell Sci. Soc. 15: 48. 1898.

Protologue typification: "Wet sandy woods, North Carolina and South Carolina. South Carolina: Cuthbert: St. Helena island. North Carolina: Ashe: Chapel Hill, June, 1898" (Ashe 1898, p. 48).

Type specimen determination by Hitchcock & Chase (1910, p. 264): "This specimen could not be found in Ashe's herbarium, but a piece of the type bearing the above data, sent by Mr. Ashe, is in the National Herbarium. It consists of a single vernal culm lacking the base, with two nodes, the blades broken off, but the sheaths present, the panicle short-exserted, the immature, pubescent spikelets 1.4 mm. long."

Types: **HOLOTYPE**: NCU 18302. **ISOTYPES**: NCU 17540; US 80524 (fragm. ex NCU 17540). Holotype designation: NCU 18302 annotated as "type" by Ashe. Label data: Herb. Rutgers College. *Panicum* ? Locality Swamp / Date 1887 / St. Helena Island, S.C. / Collector A. Cuthbert."

Commentary: NCU 18302 has been treated as a lectotype, but an Ashe note on the sheet identifies it as the "*P. cuthbertii* type." If found, any specimens matching the Chapel Hill data in the protologue would be paratypes. The obvious evidence of material removed from NCU 17540 indicates it is the source of the material on US 80524.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum ensifolium* Baldwin.

Current treatment: *Panicum ensifolium* is the basionym of *Dichanthelium ensifolium* (Baldwin ex Elliott) Gould (Freckmann & Lelong 2003, LeBlond 2019a).

14. PANICUM DELAWARENSE Ashe, North Carolina Agric. Res. Serv., Bull. 175: 116. 1900.

Protologue typification: "Dry soil near Centreville, Del. Collected by A. Commons, July 6, 1878" (Ashe 1900b, p. 116).

Type specimen determination by Hitchcock & Chase (1910, p. 156): "The type, in Ashe's herbarium, consists of four solitary culms with long-exserted, over-mature panicles, and sparsely pubescent spikelets."

Types: **HOLOTYPE**: NCU 17535. **ISOTYPE**: US 2808899 (incl. fragm. ex NCU 17535). Holotype designation: NCU 17535 annotated as "type" by Chase (see Commentary), and published by Hitchcock & Chase (1910). Label data: "HERB. A. COMMONS 48 / *Panicum Delawarense* / dry soil, (Feldspar quarries) near Centreville, Delaware. July 6, 1878. Coll. A.C."

Commentary: On NCU 17535 is a Chase note that reads, "taken as type of *P. Delawarense* Ashe." Although the sheet contains no type designation by Ashe, it is the only known specimen of the type collection from his herbarium. Isotype US 2808899 has an A. Commons label matching the protologue except that the number in the upper right portion is 358, not 48. Just to the left of "358" is a note reading "=48 W.W.A," probably by Chase, and referring to the Commons 48 specimen in Ashe's herbarium. It is apparent that Commons' numbering system applied to something other than place and date of collection. Elsewhere on the sheet is a note by Chase reading, "Dupl type agrees prefectly with type in Ashe herb." A packet on US 2808899 contains material noted as "from type in Ashe herb," and is a second isotype on the sheet.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum werneri* Scribner.

Current treatment: *Panicum werneri* is a synonym of *Dichanthelium liniarifolium* (Scribner) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

15. PANICUM DICHOTOMIFLORUM Michaux var. **PURITANORUM** Svenson, Rhodora 22: 154-156, f. 1-5. 1920.

Protologue typification: "dry sandy and gravelly beach, Half-way Pond, Barnstable, Sept. 13, 1919, *Fernald* (TYPE in Gray Herb.)" (Svenson 1920, p. 155).

Type specimen determination: There is only one specimen from the type collection at GH, and it is noted as the "TYPE." It therefore is the holotype.

Types: **HOLOTYPE**: GH 24098. **ISOTYPES**: NEBC 28645; NY 413974; US 1125005, 1223441, 1502799. **TOPOTYPE**: NCU 600438**.** Holotype designation: GH 24098 anonymously stamped as "TYPE," and published in Svenson (1920, p. 155). Label data: "PLANTAE EXSICCATAE GRAYANAE / 306. *Panicum dichotomiflorum* MICHX., Var. *puritanorum* SVENSON / Rhodora xxii. 154 (1920). Damp, sandy beach of Half-way Pond, Barnstable, Massachusetts. Coll. M.L. Fernald. September 13, 1919."

Commentary: Tropicos and NY show the Fernald collection number as 306, but based on two isotypes at US (1125005 and 1223441) it should be 17831. The "306" that appears on the Gray Herbarium labels refers to the *Plantae Exsiccatae Grayanae* series of specimens that had been distrubted to other herbaria. Half-way Pond is now called Mary Dunn Pond. Many paratypes are cited in the protologue, the majority collected by Fernald.

Current treatment: *Panicum dichotomiflorum* var. *puritanorum* (LeBlond 2019b), and *P. dichotomiflorum* subsp. *puritanorum* (Svenson) Freckmann & Lelong (Freckmann & Lelong 2003).

16. PANICUM EARLEI Nash, Bull. Torrey Bot. Club 26: 571. 1899.

Protologue typification: "Type collected at Auburn, Lee Co., Alabama, on May 7, 1898, by Messrs. F.S. Earle and C.F. Baker, no. 1532; no. 1535, of the same place and date, also belongs here" (Nash 1899, p. 571).

Type specimen determination by Hitchcock & Chase (1910, p. 267): "The type, in Nash's herbarium, consists of a tuft of early vernal culms 8 to 15 cm. high, with immature panicles. The blades are sparsely pilose on the upper surface."

Types: **HOLOTYPE**: NY 413978. **ISOTYPES**: NCU 17582, 596508; US 2808882 (fragm. ex NY 413978). Holotype designation: NY 413978 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data: "1532 Alabama Biological Survey. Type / *Panicum Earlei* Nash, sp. nov. / Auburn, Lee Co., 5/7 1898 / Coll. F.S. Earle & C.F. Baker."

Commentary: NCU 596508 is the *Earle & Baker 1535* collection cited in the protologue. Since the date and place are the same as the type collection, it is an isotype. This sheet contains four taxa: *Dichanthelium curtifolium* (Nash) LeBlond, *D. ensifolium* (Baldwin ex Elliott) Gould, *D. strigosum* (Muhlenberg) Freckmann var. *strigosum*, and *D. villosissimum* (Nash) Freckmann var. *villosissimum*. The isotype specimen is *D. curtifolium*. Hitchcock & Chase (1910, p. 267) placed *P. earlei* with *Panicum curtifolium* Nash, while Gould & Clark (1978) placed it with *D. acuminatum* (Swartz) Gould & C.A. Clark var. *implicatum* (Scribner) Gould & C.A. Clark. The differing treatments reflect the intermediacy of some plants in the type collection. NCU isotype 17582 has glabrous spikelets 1.2-1.3 mm long and bearded nodes, consistent with *D. curtifolium* (which can also have pubescent spikelets to 1.4 mm long). But the internodes as well as sheaths are spreading-hairy, and the ligules are 2-2.5 mm long. In *D. curtifolium*, the internodes are glabrous, and the ligules are 1-2 mm long. These characters suggest hybridization between entities in the *Ensifolia* and

Lanuginosa sections, but that cannot be assumed. Study is needed. The characters of *D. curtifolium* specimen NCU 596508 are consistent with *D. curtifolium* sensu stricto.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum curtifolium*.

Current treatment: *Panicum curtifolium* is the basionym of *Dichanthelium curtifolium* (LeBlond 2019a), and of *D. ensifolium* subsp. *curtifolium* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

17. PANICUM EATONII Nash, Bull. Torrey Bot. Club 25: 84-85. 1898. (Name spelled *P. eatoni* in protologue and Hitchcock & Chase 1910.)

Protologue typification: "Along the coast, Maine to New York. I take pleasure in naming this grass for Mr. Alvah A. Eaton, who sent me specimens of it collected by himself at Seabrook, N.H." (Nash 1898, p. 85).

Type specimen determination by Hitchcock & Chase (1910, p. 201): "The type, in Nash's herbarium, consists of two vernal culms with spikelets measuring 1.5 to 1.6 mm. long."

Types: **HOLOTYPE**: NY 413979. **ISOTYPE**: US 80879 (fragm. ex NY 413979 & photo). Holotype designation: NY 413979 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data: "Type / *Panicum Eatoni* Nash. Seabrook, N.H. Coll: A.A. Eaton, 1897."

Commentary: NCU specimen 17589 has been treated as a type of *Panicum eatonii*. It is from the herbarium of Alvah A. Eaton, and the label reads: "*Panicum Eatoni* Nash / Flat, swampy undrained mowing field / 7-27-'96 / Type specimen / Amesbury Mass." Neither the date nor the locality agree with the protologue and holotype label data, and Nash referenced no other collection. This specimen is not a type.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum spretum* Schultes.

Current treatment: *Panicum spretum* is the basionym of *Dichanthelium spretum* (Schultes) Freckmann (Freckmann & Lelong 2003; LeBlond 2019a).

18. PANICUM ERYTHROCARPON Ashe, J. Elisha Mitchell Sci. Soc. 16: 90-91. 1900.

Protologue typification: "The type material was collected by the writer on the sand hills of New Hanover county, N.C., May 19, 1899" (Ashe 1900a, p. 91).

Type specimen determination by Hitchcock & Chase (1910, p. 237): "The type, in Ashe's herbarium, is the vernal form, labeled, 'Shady slopes on the sand hills one mile north of Wilmington [New Hanover County] [sic], N.C.'"

Types: **HOLOTYPE**: NCU 17821. **ISOTYPES**: NCU 17822, 17823; US 2383635. Holotype designation: NCU 17821 annotated as "type" by Chase (see Commentary), and published by Hitchcock & Chase (1910). Label data: "PLANTS OF THE SOUTHERN UNITES STATES. EASTERN NORTH CAROLINA. =*Panicum ovale* Ell. Shady slope on the sand hills one mile north of Wilmington N.C., May 17, 1899, W.W. Ashe, Collector." "=*Panicum ovale* Ell." appears to have been added later over an erased name, apparently by H.L. Blomquist, whose initials appear above the label with the date: "! H.L.B. 10-28-37." The "H" looks like an "N," suggesting Nathanial Lord Brown, but Brown died in 1934. The devil truly is in the details.

Commentary: On holotype NCU 17821 is a Chase note indicating that it was "taken as type of *Panicum erythrocarpon* Ashe / data is consistent except date with that published. Published date is 19 instead of 17. Probably typographical error." Isotype NCU 17822 contains a Chase note reading

"These are same form as those in cover marked in Ashe's hand '*P. erythrocarpon* – sp. nov.' Data on label is exactly the same." Chase's use of "These" and "those" refers to the individual plants on the two specimen sheets rather than to additional sheets or unmounted material. Her comment that the data on the label of NC 17822 was "exactly the same" can only refer to the label on the specimen in the folder ("cover") marked "sp. nov.," NC 17821. Isotype NCU 17823 is labeled as a "co-type," but not by Chase or Ashe. Isotype US 2383635 agrees with the protologue, and contains a note by Chase stating that it was "from unmounted material," and thus not a fragment of the holotype. These notes argue that NCU 17821 was the only mounted and labeled specimen in the "cover marked in Ashe's hand '*P. erythrocarpon* – sp. nov.'"

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum ovale* Elliott.

Current treatment: *Panicum ovale* is the basionym of *Dichanthelium ovale* (Elliott) Gould & C.A. Clark (Freckmann & Lelong 2003, LeBlond 2019a).

19. PANICUM FILICULME Ashe, J. Elisha Mitchell Sci. Soc. 15: 59-60. 1898, nom. illeg. hom., not Hackel ex Schinz, 1895.

Protologue typification: "Dry soil, middle North Carolina to Georgia in the Piedmont plateau region. ... North Carolina: Ashe; Chapel Hill, 1898. Georgia: Small; Stone Mt., Aug. 1895" (Ashe 1898, p. 60).

Type specimen determination by Hitchcock & Chase (1910, p. 210): "The type could not be found in Ashe's herbarium. In the National Herbarium is a specimen from Stone Mountain, Georgia, collected by Ashe, which answers to the description. The culms are erect, slender, 12 to 20 cm. high, with small panicles about 2 cm long. The culms are the early autumnal form with a few erect fascicles of secondary branches. This specimen differs somewhat in aspect from the type of *P. meridionale*, but they are forms of the same species."

Types: **LECTOTYPE**: NCU 18291. **TOPOLECTOTYPE**: US 970525. Lectotype designation: NCU 18291 annotated and published by LeBlond (2015). Label data: "GEORGIA PLANTS / COLLECTED ON AND ABOUT STONE MOUNTAIN, DEKALB COUNTY / JOHN K. SMALL, AUGUST 1-6, 1895 / ALTITUDE 1000-1500 FEET."

Commentary: NCU 18291 is from Ashe's herbarium. No taxonomic name was entered on Small's label, but the specimen matches the protologue date, location, collector, and description for *P. filiculme*.

Hitchcock & Chase apparently never saw a type specimen for this name. The specimen labeled as collected by Ashe (not by Small, and without date) from Stone Mountain, and referenced by Hitchcock & Chase, was erroneously considered to be the lectotype by Lelong (1984) and Hansen & Wunderlin (1988). But it should be noted that "W.W. Ashe, Collector" on the label is printed, along with "PLANTS OF THE SOUTHERN UNITED STATES." It is possible that Ashe, who annotated this specimen on the label as "*Panicum filiculme* Ashe," carelessly used his own label for a Small specimen. Seven of the names treated in this paper were based on Small collections, four by Nash and three by Ashe. No doubt Small was sending specimens to the two most talented field taxonomists working in *Panicum* in the southeastern U.S. It is possible that the so-called Ashe specimen was collected by Small, and might have been from the type collection.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum meridionale* Ashe.

Current treatment: *Panicum meridionale* is the basionym of *Dichanthelium merdionale* (Ashe) Freckmann (LeBlond 2019a), and synonym of *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *implicatum* (Scribner) Freckmann & Lelong (Freckmann & Lelong 2003).

20. PANICUM FILIRAMUM Ashe, J. Elisha Mitchell Sci. Soc. 16: 88-89. 1900. *Panicum* "*filirameum*" is the common spelling, but "*filiramum,*" the spelling in the protologue, has been determined to be valid (Gandhi 2013).

Protologue typification: "Habitat: sandy woods, eastern North Carolina. Type material collected in New Hanover county, N.C., in June 1899" (Ashe 1900a, p. 89).

Type specimen determination by Hitchcock & Chase (1910, pp. 166-167): "The type, in Ashe's herbarium, consists of two single vernal plants, with slender, villous culms, sheaths less villous, blades nearly glabrous on one plant, sparsely long-pilose on the other, the panicles overmature."

Types: **LECTOTYPE**: US 2808880 (mounted specimen). **ISOLECTOTYPES**: NCU 18214; US 2808880 (unmounted material in packet). Lectotype designation: US 2808880 designated by LeBlond (2015). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. EASTERN NORTH CAROLINA. *Panicum filiramum* W.W. Ashe / Near Wilmington N.C. / June 1899 / W.W. Ashe, Collector."

Commentary: The type seen by Hitchcock & Chase "in Ashe's herbarium" has never been located. A Chase notation on US 2808880 identifies it as "a good match for type loaned Dec 1905." US 2808880 contains an isolectotype in addition to the mounted lectotype. The isolectotype is in a packet "from unmounted dupl. type in Ashe herb." A Chase notation on the lower left of NCU 18214 states "not type of Panicum filirameum / the type is a mounted duplicate of this in Ashe herb loaned Nat Herb Dec 1905." In other words, NCU 18214 is a "duplicate" of the now-missing type. In addition to material of *P. filiramum*, NCU 18214 also contains material currently treated as *Dichanthelium dichotomum* (L.) Gould var. *dichotomum*.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum aciculare* Desvaux.

Current treatment: *Panicum filiramum* is the basionym of *Dichanthelium filiramum* (Ashe) LeBlond (LeBlond 2019a). *Panicum aciculare* is the basionym of *Dichanthelium aciculare* (Desvaux ex Poiret) Gould & C.A. Clark (Freckmann & Lelong 2003; LeBlond 2019a).

21. PANICUM GEORGIANUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 36. 1898. (This name, thought to be blocked by *Panicum georgicum* Spreng. 1825, was superfluously replaced by *Panicum cahoonianum* Ashe, J. Elisha Mitchell Sci. Soc. 15: 113. 1899.)

Protologue typification: "Dry sandy soil, southern Georgia and Florida. ... Georgia: Small; Darden Junction, McIntosh Co., June 27, 1895. Florida: Chapman; Apalachicola" (Ashe 1898, p. 36).

Type specimen determination by Hitchcock & Chase (1910, p. 169): "The type specimen, which is in the Biltmore Herbarium and which is marked '*P. georgianum* W.W. Ashe,' in Ashe's writing, is the autumnal form."

Types: **LECTOTYPE**: US 742690. **ISOLECTOTYPES**: NCU 17706, 17707; NY 381606, 413982; US 2808870. Lectotype designation: US 742690 designated by LeBlond (2015). Label data: "GEORGIA PLANTS. COLLECTED ABOUT DARIEN JUNCTION, MCINTOSH CO. BY JOHN K. SMALL, JUNE 25-27, 1895. *Panicum Georgianum* Ashe. AT SEA LEVEL."

Commentary: Ashe misnamed the site as "Darden Junction" in the protologue. Hitchcock & Chase determined the Biltmore Herbarium specimen to be the holotype. That specimen has not been relocated. Hansen & Wunderlin (1988) interpreted the Hitchcock & Chase designation as lectotypification, stating under synonymy of *Dichanthelium ovale*: "*Panicum georgianum* Ashe ... (lectotype, US). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 169. 1910)." There are two sheets from the type collection at US, and Hansen & Wunderlin did not indicate which one they believed to be the lectotype. Neither US sheet has a *Panicum georgianum* notation in Ashe's handwriting, so neither can be the missing Biltmore holotype.

US 742690 matches the protologue, and is identified as the "Type," but not in Ashe's or Chase's handwriting. The sheet is identified as having been purchased from Scribner's herbarium by Hitchcock in 1905. This sheet was examined by Hitchcock & Chase (see following discussion of US 2808870), and the specimen placed in synonymy with *Panicum consanguineum* Kunth (which is where they placed *P. georgianum*). It is selected as the lectotype.

US 2808870 contains two plants representing two collections. The plant on the left is the autumnal form, and is designated on the sheet as "type of *P. Georgianum*." The plant on the right is the vernal form. There are separate labels for each plant, but as Chase notes, "they are doubtless transposed; the May 20 label [beneath autumnal plant] should go with the vernal culm, and June 25-27 with branching plant which is certainly of same collection as the Darien Junction June 25-27 specimen in Hitchcock herbarium [the lectotype, US 742690]." A notation in E.D. Merrill's handwriting identifies the autumnal plant as "the co-type of *Panicum georgianum*." The May 20 vernal plant, collected from Ocmulgee Swamp, has no standing as a type. Hitchcock & Chase do not mention the Florida collection cited in the protologue. Any specimen determined to be from that collection would be a paralectotype.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum consanguineum* Kunth.

Current treatment: *Panicum consanguineum* is the basionym of *Dichanthelium consanguineum* (Kunth) Gould & C.A. Clark (Freckmann & Lelong 2003; LeBlond 2019a).

22. PANICUM GLABRISSIMUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 62. 1898.

Protologue typification: "The type material was collected by me June 1898, at Manteo, Dare Co., N.C." (Ashe 1898, p. 62).

Type specimen determination by Hitchcock & Chase (1910, p. 265): "The type could not be found in Ashe's herbarium. In the Mohr Herbarium is a specimen labeled in Ashe's writing '*Panicum glabrissimum* Ashe' and bearing the cited data. This is a tuft of three vernal culms and agrees with the description, except that the spikelets are said to be glabrous, while these are pubescent. The specimen in the National Herbarium from the same station and sent by Ashe as part of the type collection is *P. tenue*, and fails in several particulars to agree with the description. While neither of these specimens is the type itself, the one which most nearly agrees with the description is taken to represent the type."

Types: **LECTOTYPE**: US 2808917. **ISOLECTOTYPES**: NY 381610, 381611. **SYNTYPES**: NCU 18009, 18013, 18014, 199964, 356867; US 971785. Lectotype designation: US 2808917 designated by Hitchcock & Chase (1910, p. 265), and annotated by LeBlond in 2012. Label data: "PLANTS OF THE SOUTHERN UNITED STATES. ON OR NEAR THE COAST OF

NORTH CAROLINA / JUNE 10- [JULY crossed out] 6, 1898. *Panicum glabrissimum* Ashe / Manteo. No. 74 in Elis. Mitch S. Society. W.W. Ashe, Collector."

Commentary: A careful reading of the Hitchcock & Chase type determination is required to identify which specimen they designated as the lectotype. The specimen "which most nearly agrees" is the one from Mohr's Herbarium, US 2808917, and thus is the specimen designated as the lectotype. Both types at NY are *P. ensifolium*, in agreement with the lectotype, and thus are isolectotypes. The label on NY 381611 reads "Roanoke Island" instead of "Manteo," but Manteo is on Roanoke Island and the label otherwise agrees with the protologue. The syntypes at NCU, along with US 971785, are *Dichanthelium tenue* (Muhlenberg) Freckmann & Lelong and thus do not agree with the lectotype.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum ensifolium*.

Current treatment: *Panicum ensifolium* is the basionym of *Dichanthelium ensifolium* (Baldwin ex Elliottii) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

23. PANICUM HAEMACARPON Ashe, J. Elisha Mitchell Sci. Soc. 15: 55-56. 1898.

Protologue typification: "District of Columbia: Kearney; 1897. Ashe: North Carolina; Chapel Hill, 1898. Iowa: Carver; Jewell Junction, 1895, No. 258" (Ashe 1898, p. 56).

Type specimen determination by Hitchcock & Chase (1910, p. 233): "The first specimen cited is chosen as the type. This is in Ashe's herbarium and consists of a tuft of three simple culms with nearly mature panicles and two autumnal culms of the previous year."

Types: **LECTOTYPE**: NCU 22518. **ISOLECTOTYPES**: NY 381618; US 314395 (incl. fragm. ex NCU 22518). **PARALECTOTYPE**: NCU 18148. Lectotype designation: by Chase annotation on NCU 22518, and published in Hitchcock & Chase (1910). Label data: "PLANTS OF THE VICINITY OF WASHINGTON, D.C. COLLECTED BY THOS. H. KEARNEY, JR. / *Panicum pubescens* Lam. / June 6 1897."

Commentary: A Chase note on NCU 22518 states: "this is type collection of *P. haemacarpon* Ashe." US 314395 contains two isolectotypes: a mounted duplicate, and a fragment of the lectotype in a packet. On paralectotype NCU 18148 is a Chase note reading: "evidently the basis of Chapel Hill N.C. Ashe citation in publication of *P. haemocarpon* Ashe. / second specimen cited."

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum villosissimum* Nash.

Current treatment: *Panicum villosissimum* is the basionym of *Dichanthelium villosissimum* (Nash) Freckmann (LeBlond 2019a), and *D. ovale* (Elliott) Gould & C.A. Clark subsp. *villosissimum* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

24. PANICUM LEUCOTHRIX Nash, Bull. Torrey Bot. Club 24: 41-42. 1897.

Protologue typification: "Type collected by the writer in the low pine land at Eustis, Lake County, Florida, in the latter part of July, 1894, no. 1338. Nos. 334 and 467, of the same collection, also belong here" (Nash 1897a, p. 42).

Type specimen determination by Hitchcock & Chase (1910, p. 205): "The type, in Nash's herbarium, consists of somewhat branching primary culms, decumbent at base. The [protologue] description reads: 'Spikelets obovate, about 0.65 mm. long, 0.4 mm. wide.' This is evidently an error, as the spikelets of the type measure 1.2 mm. as do also those of Nash 334 and 467 cited with the description."

Types: **HOLOTYPE**: NY 381627. **ISOTYPES**: MO 1837650, 1837651; NCU 17754; NY 381626; US 208336, 480512,742828, 742830. Holotype designation: NY 381627 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data: "PLANTS OF CENTRAL PENINSULAR FLORIDA, COLLECTED IN VICINITY OF EUSTIS, LAKE COUNTY BY GEO. V. NASH JULY 16-31, 1894. / 1338. *Panicum leucothrix* Nash, n. sp. / LOW PINE LAND."

Commentary: Isotype NCU 17754 has a printed and typed label indicating that the specimen is "Type material" and conforming with the protologue, except it states that it was collected by Ashe, not Nash. Under this label is another label handwritten by Ashe himself, which reads: "Type material / *P. leucothrix* Nash, Eustis, Lake Co., Fla, July 16, 1894." The typed label undoubtedly was prepared by someone other than Ashe, who presumed Ashe to be the collector. This specimen likely was sent by Nash to Ashe, a common practice among field taxonomists of that era.

No type sheets are known from "Nos. 334 and 467, of the same collection" (Nash 1897a, protologue). These specimens may be in the main collection at US. This is another example of label numbers used for purposes other than their restricted use of today.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum leucothrix*.

Current treatment: *Panicum leucothrix* is the basionym of *Dichanthelium leucothrix* (Nash) Freckmann (LeBlond 2019a), and *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *leucothrix* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

25. PANICUM LONGIFOLIUM Torrey var. **TUSKETENSE** Fernald, Rhodora 23: 192-193. 1921.

Protologue typification: "wet peaty margin of Butler's Lake, Gavelton, September 4, [1920] *Fernald, Long & Linder*, no. 19,764 (TYPE in Gray Herb.)" (Fernald 1921, p. 192-193).

Types: **HOLOTYPE**: GH 23009. **ISOTYPE**: US 1100024. **TOPOTYPE**: NCU 54029. Holotype designation: "TYPE" anonymously stamped on GH 23009, and published in Rhodora (1921, p. 193). Label data: "GRAY HERBARIUM EXPEDITION TO NOVA SCOTIA / YARMOUTH COUNTY / No. 19764 / *Panicum longifolium* Torr., var. *tusketense* Fernald, n.v. / Type no. / *Wet peaty margin of* Butler's (Gavelton) Lake, Gavelton / M.L. Fernald, B. Long, & D.H. Linder / *September 4, 1920*."

Commentary: In addition to the types referenced here, five paratype collections are cited in the protologue.

Current treatment: Plants belonging to *Panicum longifolium* var. *tusketense* are outside the range of LeBlond (2019a), and the name was not treated by Freckmann & Lelong (2003). An examination of the topotype at NCU suggests they are more closely aligned with =*P. longifolium* var. *combsii* (Scribner & C.R. Ball) Fernald than with var. *longifoliim*. *Panicum longifolium* is now treated as *Coleatania longifolia* (Torrey) Soreng subsp. *longifolia* and subsp. *combsii* (Scribner & C.R. Ball) Soreng.

26. PANICUM LUCIDUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 47-48. 1898.

Protologue typification: "Collected in June 1898 by the writer in deep, shady swamps bordering lake Mattamuskeet, N.C." (Ashe 1898, p. 48).

Type specimen determination by Hitchcock & Chase (1910, p. 198): "There is no specimen in Ashe's herbarium from the type locality, but there is a specimen of the vernal form in the National Herbarium collected by Ashe in 1898 at Lake Mattamuskeet. This specimen is either the type or a duplicate type. The label is in Ashe's handwriting."

Types: **LECTOTYPE**: US 2808887. **ISOLECTOTYPES**: NCU 570351; NY 381634, 381635. Lectotype designation: US 2808887 effectively designated by Hitchcock & Chase (1910). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. ON OR NEAR THE COAST OF NORTH CAROLINA / JUNE 10—JULY 6, 1898. / *Panicum lucidum* Ashe / Lake Mattamuskeet / W.W. Ashe, Collector."

Commentary: Since it is still unknown whether US 2808887 "is either the type or a duplicate type," it is best to continue to regard it as a lectotype. Chase noted on the sheet that the specimen was a "Co-Type." There are three specimens at NY annotated as *Panicum lucidum* isolectotypes by Gould. This designation is correct for NY 381634 and NY 381635. But NY 381636 differs in locale, date, and collector. That specimen is a syntype of *P. taxodiorum* Ashe (also treated in this paper).

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum lucidum*.

Current treatment: *Panicum lucidum* is a basionym of *Dichanthelium lucidum* (Ashe) LeBlond (LeBlond 2019a), and of *D. dichotomum* subsp. *lucidum* (Ashe) Freckmann & Lelong (Freckmann & Lelong 2003).

27. PANICUM MALACOPHYLLUM Nash, Bull. Torrey Bot. Club 24: 198. 1897.

Protologue typification: "Type collected by Mr. B.F. Bush on May 19, 1895, at Sapulpa, Indian Territory, no. 1228. The grass secured by Dr. Edward Palmer in 1868, on the False Washita, between Fort Cobb and Fort Arbuckle, Indian Territory, no. 383, belongs here. Dr. Gattinger also obtained it in the cedar barrens of Tennessee, in May, 1880" (Nash 1897b, p. 198).

Type specimen determination by Hitchcock & Chase (1910, p. 280): "The type, in Nash's herbarium, consists of two early autumnal culms 28 and 35 cm. high, with mature primary panicles."

Types: **HOLOTYPE**: NY 381641. **ISOTYPES**: MO 440022, 440023, 440024; NCU 17725; US 2808946 (fragm. & photo ex NY 381641). Holotype designation: NY 381641 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data (in Nash's handwriting): "HERBARIUM OF COLUMBIA COLLEGE, NEW YORK. *Panicum malacophyllum* Nash n. sp. COL B.F. Bush, May 19, 18985, No. 1228. Common. LOC Sapulpa, Indian Territory."

Commentary: None required.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum malacophyllum*.

Current treatment: *Panicum malacophyllum* is the basionym of *Dichanthelium malacophyllum* (Nash) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

28. PANICUM MATTAMUSKEETENSE Ashe, J. Elisha Mitchell Sci. Soc. 15: 45. 1898.

Protologue typification: "Roadsides, ditch banks and wet open woods around lake Mattamuskeet, N.C., where it grows with *P. barbulatum*. June and July. . . . Collected by the writer, and Mr. Gilbert Pearson in June, 1898" (Ashe 1898, p. 45).

Type specimen determination by Hitchcock & Chase (1910, p. 186): "The type could not be found in Ashe's herbarium. In the National Herbarium is a specimen labeled '*Panicum Mattamuskeetense* Ashe, Lake Mattamuskeet' in Ashe's handwriting, collected 'June 10-July 6, 1898,' by 'W.W. Ashe,' evidently a duplicate type. This is a single vernal culm nearly 80 cm. high, with a mature panicle, and agrees in all respects with the description except that the spikelets are described as glabrous, while those of the specimen are pubescent. The two lower sheaths and lower blade are velvety pilose; the spikelets are 2.3 mm. long. A second duplicate type in Biltmore Herbarium is a better and more characteristic specimen."

Types: **LECTOTYPE**: US 2808955. **ISOLECTOTYPES**: NCU 17718, 17721, 410427; NY 951433, 951434, 951435. **TOPOLECTOTYPE**: NCU 578243. Lectotype designation: US 2808955 effectively designated by Hansen & Wunderlin (1988, p. 1645) (see Commentary). Label data: *Panicum Mattamuskeetense* Ashe, "Lake Mattamuskeetense," June 10-July 6, 1898, *W.W. Ashe s.n.*

Commentary: Hitchcock & Chase did not state that either the Biltmore specimen or US 2808955 was "chosen" or "taken" by them as the (lecto)type in place of the missing type in Ashe's herbarium. Among these, US 2808955 is the only surviving specimen designated as a type ("co-type"), as the Biltmore specimen is also missing. Hansen & Wunderlin (1988) effectively designated US 2808955 as the lectotype by the following published statement in the synonymy of *Dichanthelium dichotomum* (Linnaeus) Gould var. *dichotomum*: "(lectotype, US; isotype, NY). Lectotypified by Hitchcock & Chase (Contr. U.S. Natl. Herb. 15: 186. 1910)." From Jan. 1, 2000 onward, the International Code of Botanical Nomenclature requires that publication of lectotypification also include the phrase "designated here" or an equivalent.

NCU 17718 has the most complete label data of the three isolectotypes at NCU from Ashe's herbarium. It may well be the missing holotype, but there is no notation on the sheet from that era identifying it as a type. The topolectotype at NCU was collected by Ashe at Lake Mattamuskeet in May 1898, a month before the lectotype collection.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum mattamuskeetense*.

Current treatment: *Panicum mattamuskeetense* is the basionym of *Dichanthelium mattamuskeetense* (Ashe) Mohlenbrock (LeBlond 2019a), and of *D. dichotomum* subsp. *mattamuskeetense* (Ashe) Freckmann & Lelong (Freckmann & Lelong 2003).

29. PANICUM MERIDIONALE Ashe, J. Elisha Mitchell Sci. Soc. 15: 59. 1898.

Protologue typification: "I have collected this species at two localities in North Carolina, Chapel Hill in June, 1898; and Jonas Ridge, Burke Co., June 1893" (Ashe 1898, p. 59).

Type specimen determination by Hitchcock & Chase (1910, p. 210): "The type could not be found in Ashe's herbarium. In the National Herbarium are two specimens, one from Chapel Hill and one from Burke County, collected by Ashe and labeled in his writing as this species. The first specimen is a tuft of very slender vernal culms, each bearing but three distant leaves, with panicles 2 to 3 cm. long. This specimen does not agree so well with the description as the Burke County plant, which is therefore chosen to represent the type. In this the culms are numerous, less delicate, erect, 10 to 15 cm. high. The spikelets are described as glabrous, but in both specimens they are minutely pubescent."

Types: **LECTOTYPE**: US 2383609. **ISOLECTOTYPE**: NCU 21629. **PARALECTOTYPE**: US 2383608. **TOPOLECTOTYPE**: US 722483. Lectotype designation: by Chase annotation, "taken as type," on US 2383609, and published in Hitchcock & Chase (1910). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. *Panicum meridionale* Ashe / Blue Ridge / Burke Co. N.C. W.W. Ashe, Collector."

Commentary: The specimen at the National Herbarium (US 2383609) designated as the lectotype identifies the location as Blue Ridge, rather than Jonas Ridge. However, Jonas Ridge is part of Blue Ridge, and it is presumed this specimen is from the same collection referenced in the protologue. The isolectotype at NCU is labeled as coming from Jonas Ridge. US 2383608 was

collected from "the vicinity of Chapel Hill, North Carolina," the other locale noted in the protologue. Topolectotype US 722483 was collected by Ashe at Jonas Ridge in July 1898.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum meridionale*.

Current treatment: *Panicum meridionale* is the basionym of *Dichanthelium meridionale* (Ashe) Freckmann (LeBlond 2019a), and synonym of *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *implicatum* (Scribner) Freckmann & Lelong (Freckmann & Lelong 2003).

30. PANICUM MICROPHYLLUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 61. 1898.

Protologue typification: "Collected by the writer June, 1898, at Chapel Hill, N.C., in moist sunny woods" (Ashe 1898, p. 61).

Type specimen determination by Hitchcock & Chase (1910, p. 210-211): "The type could not be found in Ashe's herbarium, nor any specimens so named by him. The description seems to apply to the autumnal form of *P. meridionale*, though the culms and sheaths described as 'glabrous or pubescent,' seem to indicate that some material of *P. tenue* or other species of the *Ensifolia* was mixed with it."

Types: **LECTOTYPE**: NY 381644. **ISOLECTOTYPE**: US 2383610 (fragm. ex NY 381644). Lectotype designation: NY 381644 designated by LeBlond (2015). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. IN THE VICINITY OF CHAPEL HILL, NORTH CAROLINA. *Panicum microphyllum* Ashe =*P. filiculme* Ashe / June / W.W. Ashe, Collector." "*Panicum microphyllum*" and "June" are in Ashe's handwriting, but "=*Panicum filiculme* Ashe" is in someone else's hand.

Commentary: NY 381644 contains a note, "Co-type," in Chase's handwriting, with an arrow pointing to the name *Panicum microphyllum* Ashe on the label. Doubtless this specimen was not seen by Hitchcock & Chase until after the 1910 publication, where they stated they had not seen "any specimens so named by him." The Gould annotation label from 1978 denotes this specimen as an isolectotype, apparently interpreting Hitchcock & Chase as designating the missing Ashe herbarium specimen as the lectotype.

US 2383610 contains a small fragment of the "Co-type," very likely the specimen at NY, which is the only known specimen matching the protologue.

At NCU is a specimen (17715) with a printed label identifying it as "*Panicum microphyllum* / Moist, grassy lands, Chapel Hill, Orange County, N.C. / Date May 26, 1898 / Coll. W.W. Ashe." There is just enough variance in the date ("May" instead of "June") and habitat ("Moist, grassy lands" instead of "sunny woods") to disqualify it as a type. Nonetheless, it may well have been regarded by Ashe as a paratype equivalent, with omission of its differing date and habitat from the protologue a common oversight of the time.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum meridionale* Ashe.

Current treatment: *Panicum meridionale* is the basionym of *Dichanthelium meridionale* (Ashe) Freckmann (LeBlond 2019a), and a synonym of *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *implicatum* (Scribner ex Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

31. PANICUM NASHIANUM Scribner var. **PATULUM** Scribner & Merrill, Circ. Div. Agrostol. U.S.D.A. 27: 9. 1900. (Name published as *Panicum nashianum patulum*.)

Protologue typification: "Type specimen: 1296 Robert Combs, Braidentown, Manatee County, Fla., September 3, 1898. ... Other specimens referred to this species: *Florida*: Old Town, 858, 859 Combs, 1898; Grasmere, 1169 Combs, 1898; Lake City, 132 (in part) Combs and Rolfs, 1898; Lake Alfred, T. Holm, 1893; Jacksonville, 140 T.H. Kearney, 1895. *Mississippi*: Biloxi, 4586, 4587 S.M. Tracy, 1898" (Scribner 1900, p. 9).

Type specimen determination by Hitchcock & Chase (1910, p. 274): "The type, in the National Herbarium, consists of a clump of numerous prostrate culms, 18 to 32 cm. long, with mature primary panicles and numerous branches with secondary panicles."

Types: **HOLOTYPE**: US 2808982. **PARATYPE**: NCU 17851 (Tracy 4586). Holotype designation: US 2808982 annotated as "Type," presumably by Scribner, and published by Hitchcock & Chase (1910). Label data: "Type / U.S. DEPARTMENT OF AGRICULTURE, DIVISION OF AGRISTOLOGY. *Panicum Nashianum* Scribn. var. *patulum* S & M / No. 1296. Collector: Combs. Date: 10-3, 1898. Town: Braidentown. County: Manatee. State: Fla. In fertile woods along the Manatee / not frequent."

Commentary: The holotype collection date in the protologue is Sep. 3, 1898, while the date on the sheet itself is Oct. 3, 1898. The protologue date is presumed to be in error. The paratype at NCU is *Tracy 4586* from Biloxi, MS.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum patulum* (Scribner & Merrill) Hitchcock.

Current treatment: *Panicum patulum* is the basionym of *Dichanthelium portoricense* (Desvaux ex Poiret) B.F. Hansen & Wunderlin subsp. *patulum* (Scribner & Merrill) Freckmann & Lelong (Freckmann & Lelong 2003; LeBlond 2019a).

32. PANICUM NEMOPANTHUM Ashe, J. Elisha Mitchell Sci. Soc. 15: 42. 1898.

Protologue typification: "Type material collected by the writer April, 1895, in the Penitentiary woods, Raleigh, N.C" (Ashe 1898, p. 42).

Type specimen determination by Hitchcock & Chase (1910, p. 177): "The type could not be found in Ashe's herbarium, but a specimen from the type material labeled in Ashe's handwriting is in the National Herbarium. This is a single vernal culm with an immature, partly included panicle; the spikelets are nearly or quite glabrous."

Types: **LECTOTYPE**: US 2383604. **TOPOLECTOTYPE**: NCU 17850. Lectotype designation: US 2383604 designated by LeBlond (2015). Label data: PLANTS OF THE SOUTHERN UNITED STATES / *Panicum nemopanthum* Ashe / Raleigh N.C . / April 1895 / W.W. Ashe, Collector.

Commentary: Chase designated US 2383604 as a "Co-type," and it was subsequently treated as an isotype of the missing holotype in Ashe's herbarium. Since the Ashe type has not been relocated, the US "Co-type" is selected as the lectotype. The topolectotype was collected by Ashe from Penitentiary woods on May 1, 1899.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum bicknellii* Nash.

Current treatment: *Panicum bicknellii* is the basionym of *Dichanthelium bicknellii* (Nash) LeBlond (LeBlond 2019a). It is regarded as a "putative hybrid" by Freckmann & Lelong (2003).

33. PANICUM NUDICAULE Vasey, Dept. Agric. Bot. Div. Bull. 8: 31. 1889.

Protologue typification: ""Swamps, Santa Rosa County, Fla. (A.H. Curtiss.)" (Vasey 1889, p. 31).

Type specimen determination by Hitchcock & Chase (1910, p. 179): "The type, in the National Herbarium, is the vernal form. It was collected in 'Swamps, Santa Rosa County, N.W. Florida,' in May [1886] by A.H. Curtiss (no. 3583*)."

Types: **LECTOTYPE**: US 2808984. **ISOLECTOTYPES**: NCU 437892; NY 7267, 381676; TAES; US 742715. Lectotype designation: by Hitchcock notation on US 2808984, and published by Hitchcock & Chase (1910). Lable data: "HERB. UNITED STATES DEPARTMENT OF AGRICULTURE. *Panicum nudicaule* Vasey [*consanguineum* Kunth lined out] / Locality: Florida. Collector: A.H. Curtiss. 188_."

Commentary: In their discussion of the type determination, Hitchcock & Chase refer to "The type," which usually indicates a type designated by the nomenclatorial author. But in this case, the type was "chosen" by a Hitchcock notation on the specimen sheet.

Confusion has arisen from the number appearing on the label of the type specimens from Santa Rosa County, and from the same number appearing on the label of a Curtiss collection of this taxon from Duval Co., Florida, made in April of a year not cited. A sheet at NY bears two specimens, one collected from Santa Rosa Co. (NY 7267, on the left), and one from Duval Co. (NY 381651, on the right). NY 7267 is an isolectotype, and NY 381651 has been treated as a syntype. However, the protologue and Hitchcock & Chase only refer to the collection from Santa Rosa Co., made in May, so the Duval Co. collection cannot be a type. In that era, label numbers were not always collection numbers. It is apparent that some collectors used them to refer to a catalogue or list, or to a group of specimens not necessarily united by place or date. That appears to have been the case here, with Curtiss apparently using "3583*" to refer to other collections he believed were =*Panicum nudicaule*. (The asterisk is on the label itself, applied by Curtiss. Its meaning could prove enlightening.)

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum nudicaule*.

Current treatment: *Panicum nudicaule* is the basionym of *Dichanthelium nudicaule* (Vasey) B.F. Hansen & Wunderlin (Freckmann & Lelong 2003; LeBlond 2019a).

34. PANICUM ONSLOWENSE Ashe, J. Elisha Mitchell Sci. Soc. 16: 88. 1900.

Protologue typification: "in the eastern part of Onslow county, N.C., where the type material was collected near Ward's Mill" (Ashe 1900a, p. 88).

Type specimen determination by Hitchcock & Chase (1910, p. 276): "The type, in Ashe's herbarium, is the vernal form with immature panicles, the culms glabrous or minutely puberulent, the lower blades as much as 1 cm. wide, and immature spikelets 2.4 mm. long. Other specimens in Ashe's herbarium and some distributed as *P. onslowense* and bearing the same data as the type are *P. lancearium*."

Types: L**ECTOTYPE**: US 2808968. **SYNTYPE**: NCU 18104. Lectotype designation: US 2808968 designated by LeBlond (2015). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. EASTERN NORTH CAROLINA. May, 19-20, 1899. 11. m. East of Jacksonville, Onslow Co. / W.W. Ashe, Collector."

Commentary: Great confusion exists between the typification described by Hitchcock & Chase, and the notations on the two extant type specimens. There is also confusion about the location of the designated type, and whether it is a holotype or lectotype. The Chase notation on syntype NCU 18104 reads: "type of *P. onslowense* [is] a mounted specimen in Ashe herb. loaned Nat Herb Dec

1905." I interpret this to mean that the (holo)type seen by Hitchcock & Chase was not NCU 18104, but instead another mounted specimen loaned by Ashe to the National Herbarium in 1905. If Chase had interpreted NCU 18104 as the holotype, she would not have used the phrase "a mounted specimen" etc. US 2808968, the only other known type sheet, has a U.S. Department of Agriculture label prepared by E.D. Merrill, not by Ashe, and noted by Merrill as "Portion of type sent by Ashe June 1900 [1899 crossed out]." This suggests that the mounted material on US 2808968 was either from unmounted material sent by Ashe, or from another mounted specimen sent in 1900.

Further complicating matters, the two type specimens are different taxa: US 2808968 =*P. webberianum* (*Dichanthelium webberianum*), and NCU 18104 =*P. lancearium* (*D. portoricense* subsp. *patulum*). Hitchcock & Chase recognized the presence of two taxa in their discussion of typification. The protologue matches =*P. webberianum*, which is where Hitchcock & Chase placed *P. onslowense*.

Hitchcock & Chase described the type "in Ashe's herbarium" as "the vernal form with immature panicles." This condition matches that of NCU 18104, but the remainder of their description belongs to =*P. webberianum*, not =*P. lancearium*. The vernal panicles on US 2808968 are mature. This is added evidence that neither US 2808968 nor NCU 18104 represents the "mounted specimen in Ashe herb. loaned Nat Herb Dec 1905."

Hansen & Wunderlin (1988) interpreted the Hitchcock & Chase type designation as lectotypification of a specimen at NCU. They also indicated there was at least one other type specimen ("isotype") present at NCU, but no other NCU type specimen is known. They noted that Hitchcock & Chase "clearly stated that the type is in Ashe's herbarium, now at NCU."

Regardless of interpretation, the specimen at NCU does not match the protologue while the specimen at US does, and it is selected as the lectotype. Since NCU 18104 is =*P. lancearium*, it is a syntype.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum webberianum* Nash.

Current treatment: *Panicum webberianum* is the basionym of *Dichanthelium webberianum* (Nash) LeBlond (LeBlond 2019a), and a synonym of *D. portoricense* (Desvaux ex Poiret) B.F. Hansen & Wunderlin subsp. *patulum* (Scribner & Merrill) Freckmann & Lelong (Freckman & Lelong 2003).

35. PANICUM PAMMELI Ashe, North Carolina Agric. Exp. Sta. Bull. 175: 116. 1900.

Protologue typification: "Prairies of Iowa, June" (Ashe 1900b, p. 116).

Type specimen determination by Hitchcock & Chase (1910, p. 154): "The type, in Ashe's herbarium, collected by R.I. Cratty, June 12, 1881, has spikelets 3.1 to 3.2 mm. long."

Types: **HOLOTYPE**: NCU 17879. **ISOTYPE**: US 2808966 (incl. fragm. ex NCU 17879). Holotype designation: NCU 17879 "taken as type" by Chase notation, published by Hitchcock & Chase (1910), and subsequently treated as holotype (see Commentary). Label data: "FLORA OF IOWA. *Panicum Pammeli* ["*Pammeli*" written above "*depauperatum* Muhl."] / Dry prairies, Armstrong, Emmet Co. / ["*Werneri* ?" and "*Bushii* ?" are also written on the label] / Legit R.I. Cratty. June 12, 1881."

Commentary: NCU 17879 has an Ashe label and was a mounted specimen when seen by Chase. The only other known type specimen is US 2808966. That sheet has mounted material, plus material in a packet marked "from type in Ashe herb." The label for the mounted material is in

Chase's handwriting. Below the label is a Chase note reading "from specimen in Ashe herb." NCU 17879 could not have been the source of the mounted material on US 2808966, based on the condition and amount of material on both sheets. Chase does not mention the presence of other mounted specimens in the Ashe herbarium, so the source of material for the mounted specimen on US 2808966 was likely unmounted material in the folder with Ashe's mounted specimen. This circumstantial evidence supports the continued recognition of NCU 17879 as a holotype rather than a lectotype.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum perlongum* Nash.

Current treatment: *Panicum perlongum* is the basionym of *Dichanthelium perlongum* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003). It does not occur within the range of the LeBlond (2019a) treatment.

36. PANICUM PARVIPANICULATUM Ashe, J. Elisha Mitchell Sci. Soc. 16: 87. 1900.

Protologue typification: "Collected May 20, in Onslow county, N.C. Type material is preserved in my herbarium" (Ashe 1900a, p. 87).

Type specimen determination by Hitchcock & Chase (1910, p. 265): "No specimen so labeled could be found in Ashe's herbarium, but a cover marked in Ashe's hand '*P. parvipaniculatum*' was found which contained eight sheets of unmounted material, of which two sheets (one within the fold of the other) were accompanied by a label with the following data in Ashe's writing: '*Panicum* gray spikelets? Peaty-soiled thickets sandy flatwoods and ditch banks, 10-18 miles east of Jacksonville, Onslow county, N.C. May 20, 1899.' Since these were the only specimens with locality and date according with those published, the specimens on the sheet with the label were chosen as the type, one tuft being deposited in the National Herbarium."

Types: **LECTOTYPE**: NCU 18272. **ISOLECTOTYPE**: US 2808959. Lectotype designation: by Chase notation on NCU 18272, and published by Hitchcock & Chase (1910). Label data: "PLANTS OF THE SOUTHERN UNITES STATES. EASTERN NORTH CAROLINA. *Panicum* gray spikelets? Peaty-soiled thickets sandy flatwoods & ditch banks, 10-18 miles east of Jacksonville, Onslow County, N.C. May 20, 1899, W.W. Ashe, Collector."

Commentary: The lectotype at NCU contains the Ashe label Chase found with the unmounted specimens.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum ensifolium* Baldwin [ex Elliott].

Current treatment: *Panicum ensifolium* Baldwin ex Elliott is the basionym of *Dichanthelium ensifolium* (Baldwin ex Elliott) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

37. PANICUM PARVISPICULUM Nash, Bull. Torrey Bot. Club 24: 347-348. 1897.

Protologue typification: "Type collected by Dr. John K. Small at Darien Junction, McIntosh Co., Ga., June 25-27, 1895.... I would also refer to this species the grass collected by Mr. A.H. Curtiss, near Jacksonville, Fla., on May 4, 1893, No. 4033, and distributed as *P. nitidum* Lam. The panicle and spikelets are somewhat smaller, but in other respects it agrees" (Nash 1897c, p. 348).

Type specimen determination by Hitchcock & Chase (1910, p. 205): "The type, in Nash's herbarium, consists of a tuft of mature vernal culms, beginning to branch. The culms and sheaths are appressed-pubescent, though less copiously so than is the type of *P. leucothrix*, and the panicles are

larger. In the description the spikelets are given as 1.5 mm long, but those of the type measure 1.3 mm."

Types: **HOLOTYPE**: NY 381657. **ISOTYPES**: NY 381662, 381663; US 2808956 (fragm. and photo ex NY 381657). **SYNTYPE**: NCU: 18272. Holotype designation: NY 381657 annotated by Nash as "Type," and published by Hitchcock & Chase (1910). Label data: "GEORGIA PLANTS. COLLECTED ABOUT DARIEN JUNCTION, MCINTOSH CO. BY JOHN K. SMALL, JUNE 25-27, 1895. *Panicum parvispiculum* Nash, n. sp. AT SEA LEVEL."

Commentary: Both holotype NY 381657 and isotype NY 381662 were annotated as the holotype by F.W. Gould in 1978, but NY 381657 is the only specimen annotated as the "Type" by Nash. NCU 18272, which has the same label data as the holotype, has glabrous culm internodes and sheaths above the base, as well as glabrous nodes, blade abaxial surfaces, and panicle axis. It was annotated by me to *D. longiligulatum* Nash.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum leucothrix* Nash.

Current treatment: *Panicum leucothrix* is the basionym of *Dichanthelium leucothrix* (Nash) Freckmann (LeBlond 2019a), and of *D. acuminatum* Swartz) Gould & C.A. Clark subsp. *leucothrix* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

38. PANICUM PSEUDOPUBESCENS Nash, Bull. Torrey Bot. Club 26: 577. 1899.

Protologue typification: "Type collected at Auburn, Lee Co., Alabama, May 7, 1898, by Messrs. F.S. Earle and C.F. Baker, no. 1537. Nos. 1522, 1524, 1526 and 1529, of this same collection are also referred here" (Nash 1899, p. 577).

Type specimen determination by Hitchcock & Chase (1910, p. 235): "The type, in Nash's Herbarium, is a clump of a few vernal, mostly immature culms. Some of the blades are nearly naked along the middle of the upper surface. Other specimens cited by Nash under this species, *Earle & Baker* 1522, 1524, 1526, 1529, have narrower blades than the type, with the upper surface often nearly glabrous; these represent the more usual form of the species."

Types: **HOLOTYPE**: NY 381672. **ISOTYPES**: NCU 18236, 18240; US 2383632, 2383633 (fragm. ex NY 381672). Holotype designation: NY 381672 annotated by Nash as "Type," and published by Hitchcock & Chase (1910). Label data: "1537 Alabama Biological Survey. Type. *Panicum pseudopubescens* Nash, sp. nov. Auburn, Lee Co. 5/7 1898 / Coll. F.S. Earle & C.F. Baker."

Commentary: The protologue statement that "Nos. 1522, 1524, 1526 and 1529, of this same collection" is another example of label numbers referring to something other than current use.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum pseudopubescens*.

Current treatment: *Panicum pseudopubescens* is a synonym of *Dichanthelium villosissimum* (Nash) Freckmann var. *villosissimum* (LeBlond 2019a) and the basionym of *Dichanthelium ovale* (Elliott) Gould & C.A. Clark subsp. *pseudopubescens* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

39. PANICUM PYRIFORME Nash, Bull. Torrey Bot. Club 26: 579. 1899.

Protologue typification: "Type collected by the writer in clay soil, at Orange Bend, Lake Co., Florida, March 12[-]31, 1894, no. 239. .... The following numbers of my collection of 1895 are also referred here: 2034, 2156, 2531a" (Nash 1899, p. 579).

Type specimen determination by Hitchcock & Chase (1910, p. 158): "The type, in Nash's Herbarium, consists of a clump of three culms, 15 to 45 cm. high. The description states that the blades are glabrous on the margin, but the type, as well as duplicate types in the National and Columbia University herbaria and in Hitchcock's herbarium, has several sparingly ciliate blades; the spikelets are said to be 'about 2.5 mm. long' but measure 2.2 mm."

Types: **HOLOTYPE**: NY 381673. **ISOTYPES**: MO 2526337; NY 381674; US 221672. **PARATYPE**: NCU 17975. Holotype designation: NY 381673 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data: "PLANTS OF CENTRAL PENINSULAR FLORIDA / Type / COLLECTED IN VICINITY OF EUSTIS, LAKE COUNTY BY GEO. V. NASH, MARCH 12-31, 1894. *Panicum pyriforme* Nash, sp. nov. ["*laxiflorum* Lam. / DETERMINED BY PROF. F.L. SCRIBNER." crossed out] / CLAY SOIL."

Commentary: The label data of the holotype at NY conforms with the protologue, except that "Orange Bend" is not mentioned. The only locale data on the label is the pre-printed "vicinity of Eustis." Orange Bend is seven miles west of Eustis. The label data on isotype NY 381674 also differs from the protologue, showing a date of "March 29, 1894" and a habitat discriptor, "Hammock land." The label data otherwise agrees with the holotype, including "no. 239."

The paratype at NCU is from number 2156 cited in the protologue. It was collected July 11-29, 1895, from Lake City, Florida.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum laxiflorum* Lamarck.

Current treatment: *Panicum laxiflorum* is the basionym of *Dichanthelium laxiflorum* (Lamarck) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

40. PANICUM RHIZOMATUM A.S. Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 109. 1910.

Protologue and typification, from Hitchcock & Chase (1910, p. 109): "Type U.S. National Herbarium no. 592752, collected August 18, 1905, Orangeburg, S.C., by A.S. Hitchcock (no. 450)."

Types: **HOLOTYPE**: US 592752. **ISOTYPES**: MO 742741; NY 381683. **PARATYPES**: NCU 20717, 20820, 578806. **SYNTYPE**: NCU 21047. Holotype designation: US 592752 annotated as "Type," and published by Hitchcock & Chase (1910). Label data: "AMERICAN GRASSES / FROM THE U.S. NATIONAL HERBARIUM, SMITHSONIAN INSTITUTION / 55. *Panicum rhizomatum* Hitchc. & Chase / As described by Hitchcock & Chase, North American Species of Panicum (Contr. U.S. Nat. Herb. 15: 109. 1910 / South Carolina: Orangeburg. Low sandy pine woods. (This is the type collection, *Hitchcock* no. 450.) Collector A. S. Hitchcock / August 18, 1905."

Commentary: Syntype NCU 21047 was determined by me to be closer to *Panicum anceps* var. *anceps*, and was so annotated on 6 May 2014. The other many collections referenced in the protologue are also syntypes or paratypes, but no attempt was made during this investigation to locate them (beyond NCU).

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum rhizomatum*.

Current treatment: *Panicum rhizomatum* is the basionym of *Coleataenia anceps* (Michaux) Soreng subsp. *rhizomata* (Hitchcock & Chase) Soreng (Freckmann & Lelong 2003; LeBlond 2019c).

41. PANICUM ROANOKENSE Ashe, J. Elisha Mitchell Sci. Soc. 15: 44. 1898.

Protologue typification: "Type material collected by writer in dry soil, Roanoke Island, N.C. June, 1898; also collected at Rose Bay and Mackleyville, N.C., the same month" (Ashe 1898, p. 44).

Type specimen determination by Hitchcock & Chase (1910, p. 196): "The type could not be found in Ashe's herbarium. In the Biltmore Herbarium is a specimen from Manteo, Roanoke Island, N.C., collected by Ashe, June 10, 1898, and labeled by him *Panicum roanokense* Ashe. This is a duplicate type or possibly the type. It consists of two vernal culms with mature primary panicles."

Types: **HOLOTYPE**: NCU 17962. **ISOTYPE**: NCU 17963. **PARATYPES**: NCU 24095, 356878; US 970167. Holotype designation: NCU 17962 annotated as "type" by Ashe, and published by LeBlond (2010). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. *Panicum Roanokense* type - / W.W. Ashe, Collector."

Commentary: A thorough discussion of the types of *Panicum roanokense* is provided in LeBlond (2010). Four specimens at NCU originally identified by W.W. Ashe as *Panicum roanokense* were determined to be the holotype, an isotype, and two paratypes. Two of the three specimens identified as *Panicum roanokense* in the US Type Specimen Register were determined not to be types, while the third specimen, US 970167, was confirmed to be a paratype, as currently treated.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum roanokense*.

Current treatment: *Panicum roanokense* is the basionym of *Dichanthelium roanokense* (Ashe) LeBlond (LeBlond 2019a), and *Dichanthelium dichotomum* subsp. *roanokense* (Ashe) Freckmann & Lelong (Freckmann & Lelong 2003).

42. PANICUM SCHNECKI Ashe, North Carolina Agric. Res. Serv., Bull. 175:116. 1900. (Name spelled *P. schneckii* at US.)

Protologue typification: "River bottoms, southern Indiana and Illinois. June" (Ashe 1900, p. 116).

Type specimen determination by Hitchcock & Chase (1910, p. 315): "The type, in Ashe's herbarium, consists of two culms, one sterile and one with an immature, scarcely-exserted panicle. On the accompanying label with the printed heading 'Herbarium of W.W. Ashe' is written in Ashe's hand 'Panicum Schnecki W.W. Ashe,' but no data whatever are given."

Types: **HOLOTYPE**: NCU 17932. **ISOTYPE**: US 80975 (fragm. ex NCU 17932). Holotype designation: NCU 17932 annotated as "type?" by Chase (see Commentary), and published by Hitchcock & Chase (1910). Label data: "Herbarium of W.W. Ashe / No. / *Panicum Schnecki* W.W. Ashe."

Commentary: Written on NCU 17932 in Chase's handwriting is "type?." Ashe did not specifically refer to this specimen in the protologue. As it was and is the only known specimen, and was in Ashe's herbarium, it is better treated as a holotype than a lectotype, as no selection was necessary.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum latifolium* Linnaeus.

Current treatment: *Panicum latifolium* is the basionym of *Dichanthelium latifolium* (Linnaeus) Harvill (Freckmann & Lelong 2003; LeBlond 2019a).

43. PANICUM SCOPARIOIDES Ashe, J. Elisha Mitchell Sci. Soc. 15: 53-54. 1898. (Name spelled *P. scoparioide* in protologue.)

Protologue typification: "Based on No. 283, ex Herb. A. Commons. Dry soil, Centreville, Del. June, 1873. Distributed sub nom. *P. Scribnerianum* Nash" (Ashe 1898, p. 54).

Type specimen determination by Hitchcock & Chase (1910, p. 238): "This specimen could not be found in Ashe's herbarium, but a specimen bearing the above name and data is in the National Herbarium and is doubtless the type. This consists of four vernal culms with immature panicles partly included in the uppermost sheaths."

Types: **LECTOTYPE**: US 2383638. **ISOLECTOTYPE**: NCU 18085. Lectotype designation: annotation of US 2383638 by Gould & C.A. Clark (1978). Label data: "Ex Herb. A. Commons. 283 / *Panicum Scribnerianum.* Nash. / dry soil / Centreville, Delaware, June 25, 1873."

Commentary: The comment by Hitchcock & Chase that the specimen in the National Herbarium was "doubtless the type" suggests holotype rather than lectotype designation. However, this appears to be one of those instances where "the type" refers to type material collectively. A Chase note on US 2383638 reads: "Probably type / Dupl type of *P. scoparioide* Ashe." In the 1910 treatment, there is a footnote in the type discussion of *P. scoparioides* that refers to the type treatment of *Panicum huachucae* Ashe. In that treatment is the following comment: "Such a specimen could not be found in Ashe's herbarium, but in the National Herbarium is a specimen so labeled which agrees with the description and which is doubtless the type, since Mr. Ashe visited the National Herbarium in the summer of 1898 and took notes on species of Panicum." These specimens of *P. scoparioides* and *P. huachucae* were designated as lectotypes by Gould & Clark (1978). We now know that Ashe had at least one specimen in his herbarium matching the details of the *P. scoparioides* type (here treated as an isolectotype, but possibly the holotype), and at least one specimen of *P. huachucae* that may have been treateable as a syntype. Given these circumstances, lectotype seems the appropriate designation.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum scoparioides*.

Current treatment: This name does not appear as a synonym in either Freckmann & Lelong (2003) or LeBlond (2019a). The Catalogue of New World Grasses (Tropicos.org 2014) and Gould & Clark (1978) treat the name as a synonym of *Dichanthelium acuminatum* (Swartz) Gould & C.A. Clark var. *acuminatum*. Based on a preliminary analysis of the isolectotype at NCU, it deserves more study.

44. PANICUM SUBSIMPLEX Ashe, North Carolina Agric. Res. Serv., Bull. 175:115. 1900.

Protologue typification: "Collected by Mr. A. Commons in dry rocky woods near Wilmington, Del., in August" (Ashe 1900b, p. 115).

Type specimen determination by Hitchcock & Chase (1910, p. 304): "The type, in Ashe's herbarium, consists of autumnal culms, with broadly elliptic, somewhat falcate blades 1.5 to 2.5 cm. wide, and small, few-flowered panicles, overtopped by the upper blades."

Types: **HOLOTYPE**: NCU 18029. **ISOTYPES**: MO 816401; NY 381688, 381689; US 81298 (fragm. ex NCU 18029), 81299. Holotype designation: NCU 18029 annotated as "type" by Chase, and published by Hitchcock & Chase (1910). Label data: "Herb. A. Commons. 10 / *Panicum subsimplex* W.W. Ashe / dry soil rocky woodlands. / Wilmington, Delaware / Aug 16, 1897 / Coll. A.C."

Commentary: Various numbers appear in the upper right corner of the type labels: "10" on the holotype, "10" over a crossed-out "49" on NY 381688, and "48" on NY 381689. Based on other

Commons specimen sheets, it is clear the numbers referred to something other than a collection made at a specific place and date (see Commentary under *P. delawarense*).

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum commutatum* Schultz.

Current treatment: *Panicum commutatum* is the basionym of *Dichanthelium commutatum* (Schultz) Gould (Freckmann & Lelong 2003; LeBlond 2019a).

45. PANICUM SUBVILLOSUM Ashe, J. Elisha Mitchell Sci. Soc. 16: 86-87. 1900.

Protologue typification: "Collected by the writer at Carlton, Minnesota, in August, in the simple state. Type material preserved in my herbarium" (Ashe 1900a, p. 87).

Type specimen determination by Hitchcock & Chase (1910, p. 227): "The type specimen, in Ashe's herbarium, consists of three tufts of several culms each, 15 to 30 cm. high, with leaves clustered at the base and long-exserted mature panicles."

Types: **LECTOTYPE**:. US 2383624 (fragm. & photo). **ISOLECTOTYPES**: NCU 18025; US 971092. Lectotype designation: US 2383624 designated by LeBlond (2015). Label data (from photo of missing holotype): "PLANTS OF THE SOUTHERN UNITED STATES ["SOUTHERN" crossed out]. ["EASTERN NORTH CAROLINA" crossed out] / *Panicum subvillosum* W.W. Ashe / Carlton Minn. / Aug 1899 / W.W. Ashe, Collector."

Commentary: The holotype from Ashe's herbarium has not been located. The specimen at NCU, which has been treated as the holotype, has the following Chase note: "dupl. type / *P. subvillosum* Ashe / type is a mounted specimen in Ashe herb. loaned Nat Herb Dec 1905." There is a photograph of the missing holotype on US 2383624 along with a small tuft of mounted material presumably from the holotype, and material in a packet noted as "from holotype." For these reasons US 2383624 has been selected as the lectotype. Neither NCU 18025 nor US 971092 matches the image of the missing holotype. US 971092 was also identified as a duplicate type by Chase, with the note: "from unmounted material in Ashe herb." No other type specimens are known.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum subvillosum*.

Current treatment: *Panicum subvillosum* is a synonym of *Dichanthelium acuminatum* (Swartz) Gould & C.A. Clark subsp. *fasciculatum* (Torrey) Freckmann & Lelong (Freckmann & Lelong 2003). Specimens referred to *Panicum subvillosum* do not occur within the range of LeBlond (2019a).

46. PANICUM TAXODIORUM Ashe, J. Elisha Mitchell Sci. Soc. 16: 91. 1900.

Protologue typification: "Type: K.K. McKenzie's [Mackenzie] No. 460. Hummocks in cypress swamps. Lake Charles, La., September 1890" (Ashe 1900a, p. 91).

Type specimen determination by Hitchcock & Chase (1910, p. 198): "The type, in Ashe's herbarium, is a specimen passing from the vernal to the autumnal form and showing the early branching condition."

Types: **HOLOTYPE**: NCU 18024. **SYNTYPES**: MO 1837653, 1837654; NY 381636; US 81291 (fragm. ex MO; fragm. ex Ashe herb.). Holotype designation: NCU 18024 annotated as "taken as type" by Chase from folder in Ashe's herberiam, and published by Hitchcock & Chase (1910). Label data: "PLANTS COLLECTED IN THE VICINITY OF LAKE CHARLES, LOUISIANA, BY KENNETH K. MACKENZIE. August 25 – September 10, 1898. *Panicum* / Hummocks in cypress swamp. No. 460. Frequent."

Commentary: There is much confusion and complexity among the type sheets. The complete Chase annotation on holotype NCU 18024 is: "taken as type of *Panicum taxodiorum* Ashe / '*P. Taxodiorum*' marked on cover in Ashe's hand." Ashe himself had not written "*taxodiorum*" on the sheet, but it apparently was the only mounted specimen in his "*P. Taxodiorum*" folder ("cover"). A Chase note on US 81291 indicates that material was taken "from unmounted specimen" from the same Ashe folder. Hitchcock & Chase (1910) assigned all of the type sheets to *Panicum lucidum* Ashe, but none is. The holotype itself belongs to *Dichanthelium longiligulatum* (Nash) Freckmann, while the syntypes (formerly treated as isotypes) belong to *D. dichotomum* (Linnaeus) Gould var. *dichotomum*.

Syntype US 81291 contains two fragments, one mounted, the other in a packet. The mounted fragment is noted as having come from a "duplicate type" at MO, most likely MO 1837653 based on morphology. The notation for the fragment in the packet reads: "from unmounted specimen in Ashe herb. in cover marked in Ashe's writing: '*P. taxodiorum*,' taken as type of *Panicum taxodiorum* Ashe." Her "taken as type" comment evidently refers to all the material in the folder, not just the mounted holotype. Both fragments belong to *D. dichotomum* var. *dichotomum*.

The syntype at NY has been treated as a paratype of *Panicum lucidum*, but the collection is not mentioned in the *P. lucidum* protologue. It too belongs to *D. dichotomum* var. *dichotomum*.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum lucidum*.

Current treatment: *Panicum lucidum* is the basionym of *Dichanthelium lucidum* (Ashe) LeBlond, and *D. dichotomum* subsp. *lucidum* (Ashe) Freckmann & Lelong (Freckmann & Lelong 2003). However, none of the type specimens belongs to this taxon. The holotype belongs to *D. longiligulatum* (LeBlond 2019a), and *D. acuminatum* (Swartz) Gould & C.A. Clark subsp. *longiligulatum* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003). The syntypes belong to *D. dichotomum* var. *dichotomum* (LeBlond 2019a), and *D. dichotomum* subsp. *dichotomum* (Freckmann & Lelong 2003).

47. PANICUM TRIFOLIUM Nash, Bull. Torrey Bot. Club 26: 550-551. 1899.

Protologue typification: "In sandy soil, North Carolina to northern Florida, west to Mississippi. Type collected by Dr. John K. Small, in the Oculmgee River Swamp, below Macon, Georgia, May 18-24, 1895. The following specimens are also referred here: NORTH CAROLINA: Chapel Hill, *W.W. Ashe* (distribued as *P. ensifolium*). SOUTH CAROLINA: Aiken, *H.W. Ravenel*. FLORIDA: Chapman, 1890, no. 3; Apalachicola, 1892, *Dr. Geo. Vasey*. ALABAMA: Buckley; Auburn, May 5, 1898, *Earle and Baker*, nos. 1534 and 1547a. MISSISSIPPI: *S.M. Tracy*, Biloxi, Aug. 1, 1894, no. 2865, March 28, 1898, no. 4602, April 2, 1898, no. 4612; Avondale, April 28, 1898, no. 4610; Horn Island, June 1, 1898, no. 4613" (Nash 1899, p. 550-551).

Type specimen determination by Hitchcock & Chase (1910, p. 261): "The type, in Nash's herbarium, consists of two tufts of slender vernal culms, 25 to 40 cm. high, with leafy bases and elongated internodes, the rather short-exserted panicles immature."

Types: **HOLOTYPE**: NY 381691. **ISOTYPES**: NCU 18219; US 2808942 (fragm. ex NY 381691). Holotype designation: NY 381691 annotated as "Type" by Nash, and published by Hitchcock & Chase (1910). Label data: "GEORGIA PLANTS. Collected in the Ocmulgee River Swamp, below Macon. By John K. Small, May 18-24, 1895. *Panicum* [*albo-marginatum* Nash crossed out]."

Commentary: Although the holotype fragment on isotype US 2808942 is large, and the holotype itself crowded, it does appear that material was removed from the right side of the holotype sheet.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum trifolium*.

Current treatment: *Panicum trifolium* is a synonym of *Dichanthelium tenue* (Muhlenberg) Freckmann & Lelong (LeBlond 2019a). The name was not treated by Freckmann & Lelong (2003).

48. PANICUM VILLOSISSIMUM Nash, Bull. Torrey Bot. Club 23: 149. 1896.

Protologue typification: "Collected by Dr. John K. Small in the Ocmulgee River swamp, below Macon, May 18-24, 1895. Only the early and more simple state was secured" (Nash 1896, p. 149).

Type specimen determination by Hitchcock & Chase (1910, p. 233): "The type, in Nash's herbarium, consists of several vernal culms with branches appearing, but secondary panicles not expanded. The spikelets are 2.3 mm. long."

Types: **HOLOTYPE**: NY 381695. **ISOTYPES**: NCU 18151; NY 381696; US 743139, 2383627. Holotype designation: designated on sheet by a "Type of:" label, and with "HoloTYPE" written by anonymous annotaters ("Holo" added later), and published by Hitchcock & Chase (1910). Label data: "GEORGIA PLANTS. COLLECTED IN THE OCMULGEE RIVER SWAMP, BELOW MACON. BY JOHN K. SMALL, MAY 18-24, 1895. *Panicum* [*Smallii* crossed out] *villosissimum* Nash n. sp."

Commentary: None required.

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum villosissimum*.

Current treatment: *Panicum villosissimum* is the basionym of *Dichanthelium villosissimum* (Nash) Freckmann (LeBlond 2019a), and of *D. ovale* (Elliott) Gould & C.A. Clark subsp. *villosissimum* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

49. PANICUM VIRGATUM Linnaeus var. **BREVIRAMOSUM** Nash, Bull. Torrey Bot. Club 23: 150-151. 1896. (Name published as *Panicum virgatum breviramosum*.)

Protologue typification: "Collected by Dr. Small in clay soil in the pine lands about Augusta, Georgia, where it was common , June 27-July 1, 1895" (Nash 1896, p. 150).

Type specimen determination by Hitchcock & Chase (1910, p. 92): "The type, in Columbia University Herbarium, is a slender plant with narrow panicles about 12 cm. long and 3 to 4 cm. wide, rather compactly flowered, and as a whole very like Wright's no. 183 ...."

Types: **HOLOTYPE**: NY 381697. **ISOTYPES**: NCU 18133; NY 381698; US 82405. Holotype designation: NY 381697 (Columbia University specimen) published by Hitchcock & Chase (1910) (see Commentary). Label data: "GEORGIA PLANTS. COLLECTED ABOUT AUGUSTA, RICHMOND CO. BY JOHN K. SMALL, JUNE 27-JULY 1, 1895. *Panicum virgatum breviramosum* Nash, n. var."

Commentary: Neither of the two type sheets at NY was annotated by Nash or Chase as the "type." In 2010, T. Zanoni annotated NY 381698 as the "Probable Holotype" and NY 381697 as a "Probable Isotype." However, NY 381697 contains the accession stamp of the Columbia University Herbarium, where the holotype was housed, while NY 381698 does not.

Taxonomic treatment by Hitchcock & Chase (1910): Synonym of *Panicum virgatum* var. *cubense* Grisebach.

Current treatment: *Panicum virgatum* var. *cubense* is an accepted taxon in LeBlond (2019b), and a synonym of *Panicum virgatum* in Freckmann & Lelong (2003).

50. PANICUM WILMINGTONENSE Ashe, J. Elisha Mitchell Sci. Soc. 16: 86. 1900.

Protologue typification: "The type material collected in May, 1899 on the sand hills near Wilmington, N.C., is preserved in my herbarium" (Ashe 1900a, p. 86).

Type specimen determination by Hitchcock & Chase (1910, p. 244): "The type, in Ashe's herbarium, is labeled, 'Shady slopes on the sand hills one mile to north of Wilmington, May 17, 1899. W.W. Ashe, Collector.' The plants are the vernal form with some autumnal culms of the preceding season attached."

Types: **HOLOTYPE**: NCU 18099. **ISOTYPE**: US 2383596. Holotype designation: NCU 18099 "taken for type" by Chase note, and published by Hitchcock & Chase (1910) (see Commentary). Label data: "PLANTS OF THE SOUTHERN UNITED STATES. EASTERN NORTH CAROLINA / shady slopes on the sand hills one mile to north of Wilmington, May 17, 1899 / W.W. Ashe, Collector."

Commentary: NCU 18099 was a mounted specimen with Ashe's label. US 2383596, the only other known type, was prepared "from unmounted material in Ashe herbarium in cover marked in Ashe's hand '*Panicum Wilmingtonense*.'"

Taxonomic treatment by Hitchcock & Chase (1910): *Panicum wilmingtonense*.

Current treatment: *Panicum wilmingtonense* is a synonym of *Dichanthelium ovale* (Elliott) Gould & C.A. Clark var. *addisonii* (Nash) Gould & C.A. Clark (LeBlond 2019a), and *D. ovale* subsp. *pseudopubescens* (Nash) Freckmann & Lelong (Freckmann & Lelong 2003).

Voucher specimens for invalid names

During this examination specimens were encountered that are now regarded as invalid names. These include names, lacking descriptions or without reference to specimens, are nomina nuda. Sometimes these names were listed in publications and sometimes they were entered on specimen sheets ("herbarium names"). They occasionally show up incorrectly as synonyms for valid names and associated specimens are sometimes incorrectly treated as types. Such specimens are best referred to as vouchers for invalid names. The following are those known at NCU.

Panicum biloxi – a Scribner name never published with a description and apparently never treated in synonymy. The name appears on a specimen sheet at NCU, no. 17808, as follows: "Type collection, *Panicum Biloxi* Scrib., Biloxi, Miss., 10 Aug 1899, *S.M. Tracy 6465*." On the sheet is a Chase note that reads: "Scribner never published this / *P. lancearium* Trin / =*P. Nashianum* Nash." The name is invalid and has no standing as a synonym. The specimen, while a voucher for the name, has no standing as a type. It belongs to *Dichanthelium portoricense* (Desveau ex Hamilton) B.F. Hansen & Wunderlin subsp. *patulum* (Scribner & Merrill) Freckmann & Lelong.

Panicum caricifolium – a Scribner name never published with a description. It was included as a synonym of *Panicum laxiflorum* Lamarck by Ashe (1898, p. 57), and of *P. xalapense* H. B. K. by Hitchcock & Chase (1910, p. 159). As an invalid name, it has no standing as a synonym. The name was applied by Scribner to more than one collection. Vouchers for two of these are located at NCU:

no. 17374, Washington D.C., May 1897, *Kearney* s.n.; and no. 17377, Tennessee, Cocke Co., 24 Aug 1897, *Kearney 970*. Both specimen sheets belong to *Dichanthelium laxiflorum* (Lamarck) Gould.

Panicum iowense – a published Ashe name without known type. The only data Ashe provides in the protologue is "Dry prairies, eastern Iowa to Kansas. June and July" (Ashe 1900b, p. 115). There is no reference to a collection. Hitchcock & Chase (1910) wrote: "There is no specimen in Ashe's herbarium bearing this name nor that can with any degree of certainty be connected with the description. There is a specimen of *P. praecocius* collected on dry prairies at Armstrong, Iowa, July, 1890, by R.I. Cratty, which is marked in pencil by Ashe, '*Panicum prairie*.'" At NCU is a specimen, no. 17673, matching the details of the Hitchcock & Chase description of the Cratty specimen. On it is a Chase note stating: "taken for the type of *P. Iowense* Ashe because data agrees with that published for that species." The Chase note, similar to others of hers on Ashe specimens, was undoubtedly written before the 1910 publication, where it is countermanded. While this remains an intriguing specimen, the data are insufficient to designate it as a type, and *Panicum iowense* Ashe is a nomen nudum. The Cratty specimen belongs to *Dichanthelium villosissimum* (Nash) Freckmann var. *praecocius* (Hitchcock & Chase) Freckmann.

Panicum nitidum* var. *pubescens – a Scribner name never published with a description. It was included in a list published by Kearney (1893), and was treated as a synonym of *Panicum villosissimum* Nash by Hitchcock & Chase (1910, p. 233). But as an invalid name, it has no standing as a synonym. The name was applied to two Kearney numbers, 58 and 141. A voucher specimen for *Kearney 141* is located at NCU, no. 17835. The specimen sheet belongs to *Dichanthelium villosissimum* (Nash) Freckmann var. *villosissimum*.

Note regarding the replacement name *Panicum halophilum*

Panicum halophilum Nash, in Lloyd & Tracy, Bull. Torrey Bot. Club 28: 86-87. 1901.

Nash renamed *Panicum repens* L. var. *confertum* Vasey as *P. halophilum* because the epithet "*confertum*" was blocked at species rank by *P. confertum* Desv., published in 1816. A single collection was cited by Nash in his publication of *P. halophilum* as a replacement name: "Collected on Petit Bois Island, Mississippi, by S.M. Tracy, on May 8, 1898, no. 4566, and distributed as *P. repens confertum,*" but he did not designate it as a type and explicitly included the varietal name in synonymy. Hitchcock & Chase also referred to this collection in their brief discussion of the name (p. 86). This collection was subsequently treated by some as a type collection, but it has no standing as a type. The type specimens for *P. halophilum* are the same as those for *P. repens* var. *confertum*.

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Table 1. *Panicum* sensu lato type specimens at NCU. Specimens found during 2011-2014 examination of NCU collections are indicated in boldface.

Panicum type name	type status	collector & no.	NCU
Panicum alabamense	holotype	Earle & Baker 1530	366
Panicum albemarlense	syntype	Ashe s.n.	17484
Panicum arenicola	**lectotype**	Ashe s.n.	20397
Panicum auburne	holotype	Earle & Baker 1527	17430
Panicum ciliosum	isotype	Tracy 4580	17360
Panicum columbianum	syntype	Scribner s.n.	17320
Panicum commelinifolium	**isolectotype**	Small s.n.	17318
Panicum commonsianum	**holotype**	Commons 341	17314
Panicum commonsianum	**isotype**	Commons 341	17316
Panicum cryptanthum	lectotype	Ashe s.n.	17544
Panicum cryptanthum	isolectotype	Ashe s.n.	17545
Panicum cryptanthum	isolectotype	Ashe s.n.	17546
Panicum curtifolium	**isotype**	Tracy 4598	17582
Panicum curtifolium	**isotype**	Tracy 4598	596508
Panicum cuthbertii	holotype	Cuthbert s.n.	18302
Panicum cuthbertii	isotype	Cuthbert s.n.	17540
Panicum delawarense	holotype	Commons 48	17535
Panicum dichotomiflorum var. puritanorum	**topotype**	LeBlond 1647	600438
Panicum earlei	isotype	Earle & Baker 1532	17582
Panicum earlei	**isotype**	Earle & Baker 1535	596508
Panicum erythrocarpon	holotype	Ashe s.n.	17821
Panicum erythrocarpon	isotype	Ashe s.n.	17822
Panicum erythrocarpon	isotype	Ashe s.n.	17823
Panicum filiculme	**lectotype**	Small s.n.	18291

Panicum filiramum	isolectotype	Ashe s.n.	18214
Panicum georgianum	**isolectotype**	Small s.n.	17707
Panicum georgianum	**isolectotype**	Small s.n.	17706
Panicum glabrissimum	**syntype**	Ashe s.n.	356867
Panicum glabrissimum	**syntype**	Ashe s.n.	199964
Panicum glabrissimum	**syntype**	Ashe s.n.	18009
Panicum glabrissimum	**syntype**	Ashe s.n.	18013
Panicum glabrissimum	**syntype**	Ashe s.n.	18014
Panicum haemacarpon	lectotype	Kearney s.n.	22518
Panicum haemacarpon	**paralectotype**	Ashe s.n.	18148
Panicum leucothrix	isotype	Nash 1388	17754
Panicum longifolium var. tusketense	**topotype**	Fernald 19764 et al.	54029
Panicum lucidum	**isolectotype**	Ashe s.n.	570351
Panicum malacophyllum	**isotype**	Bush 1228	17725
Panicum mattamuskeetense	isolectotype	Ashe s.n.	17718
Panicum mattamuskeetense	isolectotype	Ashe s.n.	17721
Panicum mattamuskeetense	isolectotype	Ashe s.n.	410427
Panicum mattamuskeetense	**topolectotype**	Ashe s.n.	578243
Panicum meridionale	isolectotype	Ashe s.n.	21629
Panicum nashianum [var.] patulum	**paratype**	Tracy 4586	17851
Panicum nemopanthum	**topolectotype**	Ashe s.n.	17850
Panicum nudicaule	**isolectotype**	Curtiss 3583*	437892
Panicum onslowense	syntype	Ashe s.n.	18104
Panicum pammeli	holotype	Cratty s.n.	17879
Panicum parvipaniculatum	lectotype	Ashe s.n.	18272
Panicum parvispiculum	**syntype**	Small s.n.	18272
Panicum pseudopubescens	isotype	Earle & Baker 1537	18236
Panicum pseudopubescens	**isotype**	Earle & Baker 1522	18240
Panicum pyriforme	**paratype**	Nash 2156	17975
Panicum rhizomatum	**paratype**	Tracy 3603	20717
Panicum rhizomatum	**paratype**	Tracy 4620	20820
Panicum rhizomatum	**paratype**	Curtiss 5747	578806
Panicum rhizomatum	**syntype**	Tracy 4564	21047
Panicum roanokense	holotype	Ashe s.n.	17962
Panicum roanokense	isotype	Ashe s.n.	17963
Panicum roanokense	paratype	Ashe s.n.	24095
Panicum roanokense	paratype	Ashe s.n.	356878
Panicum schnecki	holotype	unknown	17932
Panicum scoparioides	**isolectotype**	Commons 283	18085
Panicum subsimplex	holotype	Commons 10	18029
Panicum subvillosum	isolectotype	Ashe s.n.	18025
Panicum taxodiorum	holotype	Mackenzie 460	18024

Panicum trifolium	**isotype**	Small s.n.	18219
Panicum villosissimum	**isotype**	Small s.n.	18151
Panicum virgatum var. breviramosum	**isotype**	Small s.n.	18133
Panicum wilmingtonense	holotype	Ashe s.n.	18099

Table 2. NCU *Panicum* sensu lato specimens determined not to be types.

Panicum type name	**specimen status**	**collector & no.**	**NCU**
Panicum biloxi	voucher for unpublished Scribner name	Tracy 6465	17808
Panicum caricifolium	vouchers for unpublished Scribner name	Kearney s.n. Kearney 970	17374 17377
Panicum eatonii	location, date not in protologue	Eaton s.n.	17589
Panicum halophilum	replacement name for P. repens var. confertum	Tracy 4566	17966
Panicum iowense (nomen nudum)	data insufficient to designate specimen as type	Cratty s.n.	17673
Panicum microphyllum	date, habitat not in protologue	Ashe s.n.	17715
Panicum nitidum var. pubescens	voucher for unpublished Scribner name	Kearney 141	17835

Table 3. Non-NCU type specimens that were found, clarified, or lectotypified during the 2011-2014 investigation.

Panicum type name	**type status**	**collector & no.**	**herbarium**
Panicum amarulum	paratype	Tracy 6508	MO 2974815
Panicum chrysopsidifolium	paratype	Curtiss No. D	US 2808891
Panicum microphyllum	lectotype isolectotype	Ashe s.n. Ashe s.n.	NY 381644 US 2383610

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HISTORICAL AND CURRENT DISTRIBUTION OF THE STATE-ENDANGERED *TRIFOLIUM REFLEXUM* (FABACEAE) IN TENNESSEE

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ABSTRACT

The earliest literature accounts of *Trifolium reflexum* L. in Tennessee are from the period 1878-1901 and indicated presence of the species in Davidson County. In some cases, these reports were vouchered by existing herbarium specimens, but the reports and specimens apparently were overlooked in accounts of the state's flora until 1968. Recognition as a species of conservation concern came in 1999 and state-endangered status was granted in 2004. Based on verified herbarium specimens and field work, *T. reflexum* occurs, or once occurred, in seven counties across the state, usually with one known site per county. However, most collections were made more than 60 years ago and only one small population in each of two counties is known to be extant.

At least 15 species of *Trifolium* are known from Tennessee, but only two are native, each state-endangered (Tennessee Flora Committee 2015). *Trifolium calcaricum* Collins & Wiebolt is known from three counties in Middle Tennessee and one county in southwestern Virginia (Atlas of Tennessee Vascular Plants 2019; USDA NRCS 2019). *Trifolium reflexum* L., the subject of this report, is known from a few localities across the state. The species is widely distributed in midwestern USA, but occurrences are scattered eastward and it is listed endangered in Illinois, Indiana, Kentucky, and Tennessee and possibly extirpated in Maryland and Pennsylvania (Chapel & Vincent 2013; USDA, NRCS 2019). Recent publications have provided historical information and current distributions for Kentucky (Campbell et al. 1988; Vincent 2001) and Ohio (Vincent 1991). Extensive descriptions and habitat preferences can be found in Vincent (1991, 2001) and Isely (1990, 1998), among others.

The objectives of this study are (1) to summarize literature concerning *T. reflexum* in the state, especially noting the publication history leading to the current designation of endangered, and (2) to document the known distribution of the species in Tennessee based on verified herbarium specimens.

Literature was accumulated from published accounts, from various databases, and from theses obtained from lending libraries. Records from the Natural Heritage Program, Tennessee Department of Environment and Conservation, were made available by concerned and helpful personnel. Herbaria within Tennessee were visited or curators contacted for information. Several out-of-state herbaria were contacted, especially those indicated by the Southeast Regional Network of Expertise and Collections (SERNEC) database to include Tennessee specimens of *T. reflexum*.

Review of Tennessee literature

The Killebrew-Gattinger Years. The first observed mention of *Trifolium reflexum* for the state was that of J.B. Killebrew (1831-1906), Tennessee's first Commissioner of Agriculture beginning in 1872. In a book dealing with Tennessee grasses and forage plants, Killebrew (1878) noted that *T. reflexum* was a "valuable forage species found round Nashville." This work was later expanded (Killebrew 1898) and when referring to pastures, he noted that "the wild clovers are numerous and nutritious, including Buffalo Clover (*Trifolium reflexum*)." Apparently, these reports were not vouchered with specimens, but Killebrew credited A. Gattinger (see next) with providing information on native species.

Augustin Gattinger (1825-1903) is recognized as the premier botanist for the state (Oakes 1932; Bishop and Priestley 2015). His first list of Tennessee vascular plants (Gattinger 1887) noted that *T. reflexum* was found in "Cedar barrens, rocky hills along Franklin Pike, Nashville" and as one of several "plants of the glades and bluffs." Gattinger later noted (1901) the presence of *T. reflexum* along "Banks of Cumberland River, below Nashville." His personal collection was sold to the University of Tennessee before his death but was lost when the entire Tennessee herbarium was destroyed by fire in 1934. However, Gattinger had exchanged specimens, or more often sent specimens as gifts, to several in- and out-of-state herbaria and colleagues (Oakes 1932). About 300 of these specimens, including two of *T. reflexum* (see citations), have returned as a result of purchases or gifts and now are on deposit at TENN (B.E. Wofford, pers. comm., 29 March 2019).

The Sharp Years. A.J. Sharp (1904-1997), long-time Professor at The University of Tennessee, apparently prepared the first list of Tennessee rare plants (Sharp 1948). That list of 25 species included "wildflowers that are in danger of becoming extinct in Tennessee." Later, Sharp (1974) expanded the list to about 90 species that included "most of the rare or threatened plants in Tennessee." Jesse M. Shaver (1888-1961), Professor at George Peabody College in Nashville (now a part of Vanderbilt University) and colleague of Sharp, published a listing of about 15 species (Shaver 1957) that he considered rare. None of these publications, or the eventual checklist of Tennessee vascular plants (Sharp et al. 1960) and addendum (Sharp & Baker 1964), included *Trifolium reflexum*. Apparently there were no *T. reflexum* specimens at TENN prior to 1964.

William Mahler (1930-2013) completed a doctoral program mentored by Sharp that included a dissertation on the legumes of the state (Mahler 1968). Distribution data were obtained mostly from specimens found in Tennessee herbaria and *Trifolium reflexum* was mapped from Davidson County. Apparently, a Gattinger collection had been located elsewhere and returned to TENN, although records are lacking and Mahler did not document sources. A revised publication (Mahler 1970) added Lewis and Madison counties. Again, vouchers were not cited, but apparently the specimens identified later in this report were the sources for the two additional counties.

Recent Years. The USDA, Soil Conservation Service (1975) published a list of about 100 Tennessee rare species. The apparently in-house list was prepared "with assistance from several Tennessee universities and other federal agencies" and did not include *T. reflexum*. An *ad hoc* committee of mostly East Tennessee botanists (see literature cited, Committee for Tennessee Rare Plants, for membership) met in 1976 and developed a list of rare species. The list was published (Committee for Tennessee Rare Plants 1978), but *T. reflexum* was not recognized.

In 1980 a Scientific Advisory Committee (SAC) of 11 state-wide botanists was appointed by the Commissioner, Tennessee Department of Conservation (now Department of Environment and Conservation) to assist the Department's Heritage Program in developing an "official" categorized list of Tennessee rare plants and to update/revise the list every third year. Paul Somers, State Botanist at the time, chaired the Committee which first met in January 1981 (correspondence in the author's files). Revisions suggested by the SAC, which meets each thrid year, are included in an updated list under the direction of the state botanist. *Trifolium reflexum* was not recognized in the SAC's early deliberations or in the first journal-published list (Somers 1989). The soon-developed Wofford and Kral (1993) checklist included the species but without rarity designation.

Recognition as a rare entity in the state came when Dr. Eugene Wofford, then TENN Curator, contacted Carl Nordman, then State Botanist, and suggested recognition of Special Concern (e-mail from Wofford to Nordman on 14 May 1998, on file Tennessee Natural Heritage Program, copy author's files). That status was assigned in the official list of October 1999, and then elevated to Endangered in 2004 under the leadership of then State Botanist Claude Bailey (personal communication with Todd Crabtree, current State Botanist). Endangered status has continued in subsequent and the current list

(Tennessee Natural Heritage Program 2016) and in state-wide accounts of the flora (Atlas of Tennessee Vascular Plants 2019; Chester et al. 1997, 2009; Tennessee Flora Committee 2015).

Summary

Literature reports for the period 1878-1901 indicate the presence of *Trifolium reflexum* in Davidson County. Some reports are supported by vouchers, but the species did not appear in later Tennessee literature until 1968. Its recognition as a species of conservation concern began in 1999 (designated special concern) and 2004 (designated endangered). Verified collections are from seven Tennessee counties ranging across the state. Collections possibly are from two sites in Davidson County and one site in other reported counties. However, collections are historic from the following five counties (the number of years since the last collection is given in parentheses): Davidson (121), Lewis (74), Madison (59), Montgomery (45), Shelby (99), or an average of 80 years. Label data are vague for four counties, making site relocation impossible; the Montgomery County site, with good location data, was visited in 2018 without success in locating representatives. Blount and Polk counties, with one known site in each, represent known extant populations.

Verified collections data

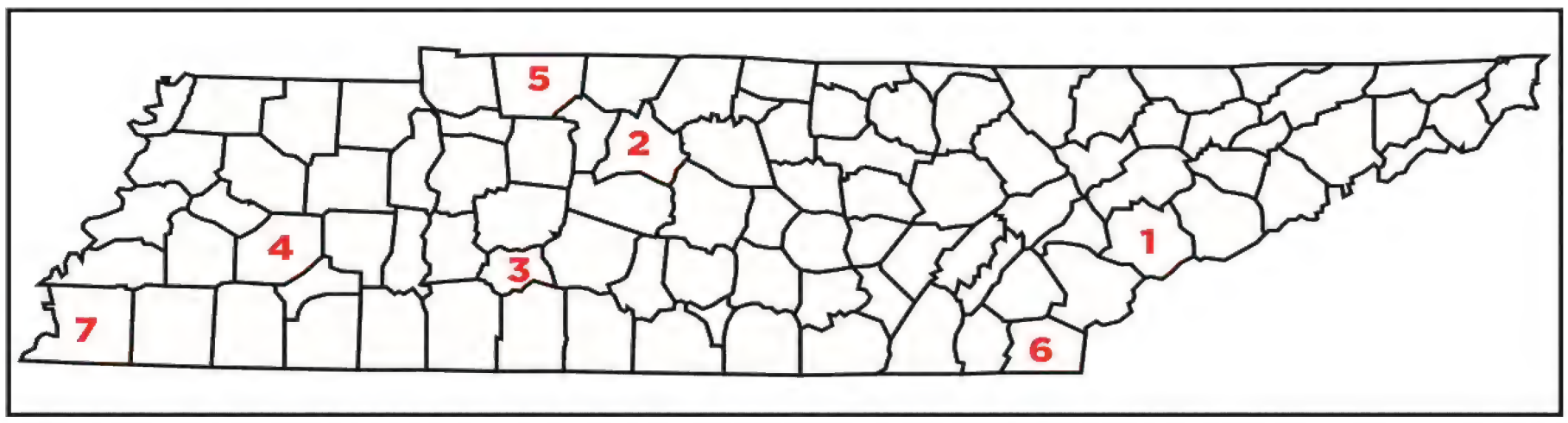

Figure 1. Tennessee counties with verified collections of *Trifolium reflexum* (see list of vouchers numbered by county).

Blount Co. (1): Calderwood Quad, dry woods at intersection of Highway 129 and gated road to Calderwood Dam, overlook pull off, 13 May 1998, *Wofford and Clebsch 98-18* (TENN, examined June 2017, duplicate at LSU reported by SERNEC, not seen; TENN specimen annotated M. Vincent 1999). Recent visits by others verified the continued presence of the species at the site (Todd Crabtree, current State Botanist, pers. comm., 26 October 2017).

Davidson Co. (2): Dry pastures, May 1878, *Gattinger s.n.* (TENN, image APSC; annotated W. Mahler 1968 and M. Vincent 1994); rocky ground around Nashville, 1898, *Gattinger s.n.* (TENN, image APSC; duplicate CM, image APSC; both originals and duplicate annotated M. Vincent 1991).

Lewis Co. (3): Little Swan Creek, Meriwether Lewis National Monument, roadside in low woods, 25 May 1945, *King 110* (VDB at BRIT, image APSC; annotated W. Mahler 1968 and R. Kral 1993).

Madison Co. (4): Near Jackson, 18 May 1960, *Shelby, s.n.* (TENN, examined June 2017; annotated W. Mahler 1968 and M. Vincent 1994). Extensive collecting for a floristic survey of the county (Beardsley 1973) did not locate the species.

Montgomery Co. (5): Shaded roadside on road to Hematite Public Use Area, 21 May 1974, *Chester 2711* (APSC, examined January 2019, and TENN, examined June 2017; both annotated M. Vincent 1994). The Public Use Area was closed in the 1980s and the gated road now is little-used; the roadside site has succeeded into dense thickets and *T. reflexum* was not observed when visited in 2018.

Polk Co. (6): North edge of Clemmer trail, right on trail edge, 14 May 2013, *Shaw and Estes s.n.* (UTCH, image APSC). This site is remote and although not recently visited, continued presence of the species is expected (D. Estes, pers. comm., 5 March 2019).

Shelby Co. (7): Open woods, moist ground along small stream near Memphis, 12 May 1920, *Palmer 17450* (MO, image APSC). Extensive collecting for a floristic survey of the county (Thompson 1975) did not locate the species.

SERNEC reports based on misidentifications.

Obion Co.: Walnut Log lawn, 27 Apr 1941, *Eyles 7740* (GEO, image APSC). The sheet label indicates "O'Brien County, Pennsylvania." However, Walnut Log is a community on the east side of Reelfoot Lake and the former site of a field station managed by the Tennessee Academy of Science. Eyles did a floristic study of the area (Eyles & Eyles 1943), working out of the Academy field station, and this specimen was probably part of that study although the number is not included in the publication. The specimen appears to be *T. repens* L.

Weakley Co.: Roadside, Hwy 22, 8 May 1974, *Bansler 137* (UTM, observed November 2018). The specimen is *T. pratense* L.

White Co.: Near Doyle, along roadsides, 11 Jul 1963, *Sparkman 14* (HTTU, image APSC). The specimen appears to be *T. pratense* L.

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Special thanks to Todd Crabtree, State Botanist with the Tennessee Department of Environment and Conservation, Natural Heritage Program, for providing collection records and materials related to the listing of *T. reflexum* as a species of conservation concern. Appreciation is extended to the Interlibrary Loan Department, Woodward Library, Austin Peay State University, for obtaining loans and to the lending libraries for the following: (1) the Beardsley and Thompson theses from the University of Memphis, and (2) the Mahler dissertation from the University of Tennessee. The following curators examined their collections and supplied images: Bonnie Isaac (CM); Aaron Floden (MO); Shawn Krosnick (HTTU), Tiana Rehman (BRIT), Tharanga Samarakoon (GEO), and Joey Shaw (UTCH). Additionally, D. Estes (APSC), B. Eugene Wofford (TENN), and Lisa Krueger (UTM) hosted visits and provided access to collections under their curation. David Johnson, Media Services at Austin Peay State University, prepared Figure 1. Appreciation is extended to Claude Bailey, formerly Tennessee State Botanist and presently Associate Professor, Jackson State Community College, Jackson, Tennessee, for reviewing the manuscript and making helpful comments.

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TOIYABEA (ASTERACEAE: ASTEREAE) ENLARGED TO INCLUDE FOUR SPECIES

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ABSTRACT

The genus *Toiyabea* is enlarged from a single species to include four: *Toiyabea alpina* (Anderson & Goodrich) Roberts et al., **Toiyabea eximia** (H.M. Hall) Nesom, **comb. nov.**, **Toiyabea peirsonii** (Keck) Nesom, and **Toiyabea granitica** (Tiehm & Shultz) Nesom, **comb. nov.** Three first three species are tightly coherent in geography and in morphology but in 2006 FNA treatments were placed in three separate genera, *Toiyabea*, *Tonestus*, and *Lorandersonia*, weighting interpretations of molecular data. The fourth, while morphologically divergent, is part of the geographic group and shares features indicative of a close relationship. A taxonomy hypothesized here to best reflect the evolutionary history recognizes all four as congeneric. The morphological and geographic evidence suggests that DNA data need to be supplemented and interpretations reexamined.

The genus *Toiyabea* was established by Roberts et al. (2005) to include the single species *Haplopappus alpinus* = *Tonestus alpinus* (nomenclatural details below). The present discussion points out that species originally named as *Haplopappus eximius* and *H. eximius* subsp. *peirsonii* are closely similar to each other and apparently inextricably related to *H. alpinus*. These taxa are referred to below as "**eximius**," "**peirsonii**," "**alpinus**," and the "**eximius trio**."

A fourth species, *Haplopappus graniticus* = *Tonestus graniticus*, also appears to be part of this group. It shares herbaceous perennial, taprooted habit, coarsely toothed leaves, herbaceous phyllary apices, and vestiture of long, erect, multicellular hairs, some of which are stipitate-glandular, and it is endemic to southwestern Nevada in close proximity to the **eximius trio**. In leaf and head arrangement and involucral morphology, however, it is distinct from the **eximius trio**. It might be given separate taxonomic standing at generic rank, or it might be considered as congeneric with the other three, alternatives considered here.

Three species

Hall (1915) noted that the affinities of his new species *Haplopappus eximius* are with *H. lyallii* A. Gray and *H. pygmaeus* (Torr. & Gray) A. Gray, differing in its deeply toothed leaves and more foliaceous involucral bracts. He also noted similarities of **eximius** to *Haplopappus aberrans* A. Nels. The second taxon, **peirsonii**, was originally described by Keck (1940) as a "very distinct geographic subspecies" of *Haplopappus eximius*, emphasizing the larger leaves, involucres, and florets of **peirsonii**. In raising its rank to species, Howell (1950, p. 87) noted that between the two taxa there were "a few small qualitative differences but in all parts there are marked quantitative differences, [*Haplopappus*] *peirsonii* being larger and coarser than [*Haplopappus*] *eximius*. These differences …, taken together with the geographic separation of the two plants, would seem to indicate that we are concerned with two distinct but closely related species."

Anderson (1980) thought the new species *Haplopappus alpinus* to be most closely related to **eximius**, to *Haplopappus aberrans*, and less closely so to **peirsonii** — weighting the eradiate heads of *H. aberrans* as an indication of relationship to **alpinus**. In placing the **eximius trio** in the genus *Tonestus*, Nesom and Morgan (1990) noted that the three species comprise a distinct morphological subgroup characterized by stipitate-glandular vestiture, toothed leaves, and phyllaries in 3-4 nearly equal series.

Haplopappus aberrans is endemic to a small area in Idaho and adjacent Montana. Although it has stipitate-glandular vestiture and toothed leaves, the leaf margins are spinulose-serrate, involucres are nearly cylindric, phyllaries are narrowly lanceolate and strongly imbricate, and the pappus is 2-seriate, among other differences from the **eximius trio**. Nesom and Morgan (1990) placed *H. aberrans* in *Tonestus* but in a different subgroup from the **eximius trio**. Molecular data indicate that *H. aberrans* is sister to subtribe Machaerantherinae (or justifiably included within the subtribe), distantly related to the **eximius trio** (subtribe Solidagininae), and it has been segregated as the monotypic genus *Triniteurybia* (Brouillet et al. 2004).

As a group, the three species considered here are characterized as perennial, taprooted herbs often with caudex branches, densely villous-glandular stems, leaves, and bracts, distinctively shaped and coarsely toothed leaves subclasping at base, one or few heads, campanulate involucres, foliaceous-herbaceous phyllaries in 3–4 series of subequal length, yellow rays (rays absent in **alpinus**), terete achenes, and terete, apically attenuate pappus bristles in a single series. The chromosome number of each is based on x = 9 (**alpinus**, $2n = 18$; **eximius**, $2n = 18$; **peirsonii**, $2n = 90$) (Howell 1950; Anderson 1980). Each occurs in rocky alpine to subalpine habitats and each is narrowly distributed in the same general region of the western USA (Fig. 2) — central Nevada (**alpinus**) and the sierra of east-central California (**eximius** and **peirsonii**).

Three species asunder

Taxonomic treatments in the Flora of North America North of Mexico have placed each of these three species in a different genus: *Toiyabea alpina* (Urbatsch et al. 2006a), *Tonestus eximius* (Morse 2006), and *Lorandersonia peirsonii* (Urbatsch et al. 2006b). Their taxonomic dispersal is underlain primarily by molecular data and its interpretations (Roberts 2002; Roberts et al. 2004; Roberts et al. 2005; Urbatsch et. al 2005).

Morse (2006) treated **eximius** within *Tonestus* but deferred to DNA interpretation regarding **peirsonii**, noting that "… while morphologic evidence indicates that *Tonestus eximius* and *Tonestus peirsonii* are closely related, the work of Roberts and Urbatsch placed the decaploid *T. peirsonii* in a clade with members of *Lorandersonia*, wherein it is treated here" (p. 182).

In treating **peirsonii** as a species of *Lorandersonia*, Urbatsch et al. (2005, p. 1623) noted that it is "a morphologically divergent species in an otherwise relatively uniform genus. … Even more puzzling than *Lorandersonia peirsonii*'s overall dissimilarity to other *Lorandersonia* is its great similarity to *Tonestus eximius*." They obtained DNA sequences for **peirsonii** "from different specimens at different times with different stock reagents" but results still were essentially identical.

Molecular analyses by Roberts and Urbatsch (2004) and Roberts et al. (2005) show **alpinus** to be within a clade also including *Petradoria pumila* and the sister species *Stenotus acaulis* and *Stenotus armerioides*, although "the position and relationships among the four taxa in that lineage were not congruent across analytical methods or data sets" (Roberts et al. 2005, p. 1648). Bayesian analysis of combined ETS and ITS data sets (their Fig. 1) show an unresolved trichotomy (pumila, alpinus, acaulis/armerioides). Roberts et al. concluded that "The two species of *Stenotus* are morphologically distinctive from *Petradoria* and merit continued recognition at generic rank. We propose *Toiyabea* to accommodate *Tonestus alpinus* because of its [morphological] distinctiveness from *Petradoria* and *Stenotus* and its failure to aggregate with any specific taxon in the sequence-based analyses."

Toiyabea alpina emerges as isolated in the morphological key by Roberts et al. (2005, p. 1654), but that is because neither **eximius** nor **peirsonii** was included among the taxa to be identified. Similarly, **eximimus** and **alpinus** were not included in the morphological key that distinguishes *Lorandersonia peirsonii* (Urbatsch et al. 2005; the terminal taxon in the key [p. 1628] was mistakenly identified as "*Lorandersonia eximius*" instead of *Lorandersonia peirsonii*).

In the 2006 Flora of North America key to genera, *Toiyabea* is separated from **eximius** and **peirsonii** on the basis of its discoid heads. The key identifies **eximius** within *Tonestus*, as expected by morphology, but **peirsonii** must be assessed as a shrub or subshrub in order to key out as a member of *Lorandersonia*. In the species descriptions, each *Lorandersonia* species is characterized as a "shrub" or "subshrub" except for *L. peirsonii*, which is correctly characterized (Urbatsch et al. 2006b, p. 179) as a "perennial" (vs. shrub or subshrub).

Three species reunited

Urbatsch (2012), without comment, returned both **eximius** and **peirsonii** to the genus *Tonestus*, implicitly acknowledging that a weighted reliance on molecular evidence led to untenable conclusions. Based on morphology and geography, a close relationship between these two species seems beyond dispute. **Alpinus** essentially differs only in its lack of ray flowers. Within *Tonestus* (*Tonestus lyallii*, the type), however, these three are morphologically and geographically disparate, and joining them within the genus *Toiyabea* (*T. alpina*, the type) provides an effective way of recognizing their coherence. A review of *Tonestus* sensu stricto is underway (Nesom, in prep. — a treatment including several previously undescribed species).

It is plausible that the decaploid genome of **peirsonii** includes a chromosome set from some other species — molecular data associate it with species of *Lorandersonia* but none of those species are sympatric with **peirsonii** and there is nothing about it to suggest genetic influence of a morphologically disparate species. Molecular data indicate that the diploid **alpinus** is related to *Petradoria* and *Stenotus* while morphology and geography place it as closely similar to **eximius** and **peirsonii**. Molecular data indicate that **eximius** is unresolved in relationship or else related to *Amphipappus* and *Chrysothamnus*, and the molecular placement of *H. graniticus* (below) is similar. Positions of these species in molecular analyses used as guides for taxonomic decisions (Roberts 2002; Roberts et al. 2004; Roberts et al. 2005; Urbatsch et. al 2005) make little sense in light of morphological patterns. In the perspective here, the only thing that can be confidently concluded from molecular data regarding these species and others of *Tonestus* (sensu Nesom & Morgan 1990) is that they are members of subtribe Solidagininae of the western USA and are essentially unresolved in placement.

Where does *Haplopappus graniticus* belong?

Haplopappus graniticus (= *Tonestus graniticus*) has been maintained within *Tonestus* by Morse (2006), although he noted (p. 182) that it was included in the genus "mostly as a matter of convenience" because of its divergent morphology. Its leaf morphology and vestiture, however, and its close geographic proximity to the **eximius trio**, indicate that its ancestry lies with those species.

Similarities exist between *Haplopappus graniticus* and **alpina** — both are endemic to isolated mountains of Nevada (vs. the Sierra Nevada distribution of **eximia** and **peirsonii**), both have a tendency to produce numerous heads per stem (compared to the usual single-headed stems of **eximia** and **peirsonii**), and heads of both lack ray flowers (heads of **eximia** and **peirsonii** are radiate). While these features of *H. graniticus* and **alpinus** might be convergent, the parsimonious choice is to regard them as indicative of a sister relationship — the reduced cauline leaves, smaller heads with fewer disc flowers, graduated, less herbaceous phyllaries, and divergent vestiture of *H. graniticus* to be interpreted as autapomorphies.

If the phylogenetic hypothesis here (Fig. 1) is correct, or even if *Haplopappus graniticus* might prove to be sister to the other three, treating all four as congeneric appears to be the more informative taxonomic option. *Haplopappus graniticus* as a monotypic genus might be more pragmatic (a 3-species *Toiyabea* would be more coherent morphologically), but a 4-species *Toiyabea* recognizes their immediate common ancestry and alludes to the apparent saltational changes in *H. graniticus*.

TOIYABEA Roberts, Urbatsch, & Neubig, Sida 21: 1653. 2005. **TYPE**: *Toiyabea alpina* (Anderson & Goodrich) Roberts, Urbatsch, & Neubig

1. *Toiyabea alpina* (Anderson & Goodrich) Roberts, Urbatsch, & Neubig, Sida 21: 1653. 2005. *Haplopappus alpinus* Anderson & Goodrich, Great Basin Naturalist 40: 73. 1980. *Tonestus alpinus* (Anderson & Goodrich) Nesom & Morgan, Phytologia 68: 177. 1990. **TYPE**: **Nevada**. Nye Co.: Slopes of 11,077 ft peak of Toiyabe Crest between Washington Creek and Aiken Creek near county line, 24 air mi SSW of Austin, among white granitic rocks, 10,600 ft, locally established with *H. macronema*, *Chrysothamnus viscidiflorus*, *Erigeron compositus*, and *Eriogonum umbellatum*, 21 Jul 1979, *L.C. Anderson 4885* (holotype: BRY; isotypes: GH, MO, NY, RSA). Figures 5-7.

2. **Toiyabea granitica** (Tiehm & Shultz) Nesom, **comb. nov.** *Haplopappus graniticus* Tiehm & Shultz, Brittonia 37: 165. 1985. *Tonestus graniticus* (Tiehm & Shultz) Nesom & Morgan, Phytologia 68: 178. 1990. **TYPE**: **Nevada**. Esmeralda Co.: Lone Mountain, Springdale Canyon on the NE side of the range, ca 14 mi W of Tonopah, T2N, R40E, in steep, granite rock outcrops, 7800 ft, 12 Sep 1983, *A.J. Tiehm 8346* (holotype: NY; isotypes: BRY, CAS, COLO, CS, FSU, G, GH, MO, NSMC, ORE, OSC, RENO, RM, RSA, TEX, US, UTC, WTU). Figures 8-13.

Additional collections. **Nevada**. Esmeralda Co.: Lone Mt. area, ca. 14 mi W of Tonopah, Springdale Canyon on the E side, steep granite rock outcrops, 7800 ft, forming clumps to 3 dm across, 30 Jul 1983, *Tiehm 8252* (ASU, KANU, NY, RM); Lone Mtn area, Springdale Canyon on the NE side of the range, ca 14 mi W of Tonopah, steep granitic rock walls, 7800 ft, 21 Jul 1984, *Tiehm 9072* (NY); Lone Mtn, Springdale Canyon on the NE side, T2N R40E S16, 38° 01' 38.9" N 117° 29' 00.3" W, steep volcanic rock outcrops, 7100 ft, forming clumps, 9 Sep 2006, *Tiehm 15338* (NY, RENO, UNLV).

3. **Toiyabea eximia** (H.M. Hall) Nesom, **comb. nov.** *Haplopappus eximius* H.M. Hall, Univ. Calif. Publ. Bot. 6: 170, f. 2, pl. 20. 1915. *Tonestus eximius* (H.M. Hall) Nelson & Macbr., Bot. Gaz. 65: 70. 1918. **TYPE**: **California**. El Dorado Co.: 1/2 mi SSW of Angora Peak, crevices of granitic rock on N side of summit of 8800 ft, 8800 ft, Jul 1910, *G.R. Hall s.n.* (holotype: UC; isotypes: GH, NY, US). Figures 14-16.

4. **Toiyabea peirsonii** (Keck) Nesom, **comb. nov.** *Haplopappus eximius* subsp. *peirsonii* Keck, Madroño 5: 169. 1940. *Haplopappus peirsonii* (Keck) J.T. Howell, Leafl. W. Bot. 6: 86. 1950. *Tonestus peirsonii* (Keck) Nesom & Morgan, Phytologia 68: 178. 1990. *Lorandersonia peirsonii* (Keck) Urbatsch, Roberts, & Neubig, Sida 21: 1623. 2005. **TYPE**: **California**. Inyo Co.: Transverse Ridge, Rock Creek Lake Basin, rock crevices, abundant at this location, 11,100 ft, 5 Aug 1933, *F.W. Peirson s.n.* (holotype: UC; isotype: DS, as cited by Keck). Figures 17-22.

Key to the species of *Toiyabea*

1. Heads discoid, (1–)2–11 per stem; isolated ranges in south-central Nevada.
   2. Heads (1–)2–4(–5) per stem; vestiture of multicellar, stipitate-glandular hairs; cauline leaves about the same size as the basal; involucres 10–12 mm wide (pressed); disc flowers 30–55; phyllaries mostly herbaceous, in 3–4 series of equal or subequal length ..... **Toiyabea alpina**
   2. Heads (1–)2–11 per stem; vestiture of multicellar hairs sharp-pointed and eglandular at apex, mixed with stipitate-glandular hairs; cauline leaves greatly reduced in size from the basal; involucres narrowly campanulate to narrowly turbinate, 4.5–7 mm wide (pressed); disc flowers 13–23; phyllaries with proximal 2/3 whitish-indurate and apical region green, in (3–)4–5 series strongly graduate in length ..... **Toiyabea granitica**

1. Heads radiate, 1(–2, rarely –4) per stem; Sierra Nevada of California and adjacent Nevada.
   3. Basal leaves 2–4 cm long, 12–15 mm wide; involucres 9–16(–20) mm wide (pressed); rays 10-13; $2n = 18$ ..... **Toiyabea eximia**
   3. Basal leaves 3–8 cm long, 12–25 mm wide; involucres (15–)20–28 mm wide (pressed); rays 16-20; $2n = 90$ ..... **Toiyabea peirsonii**

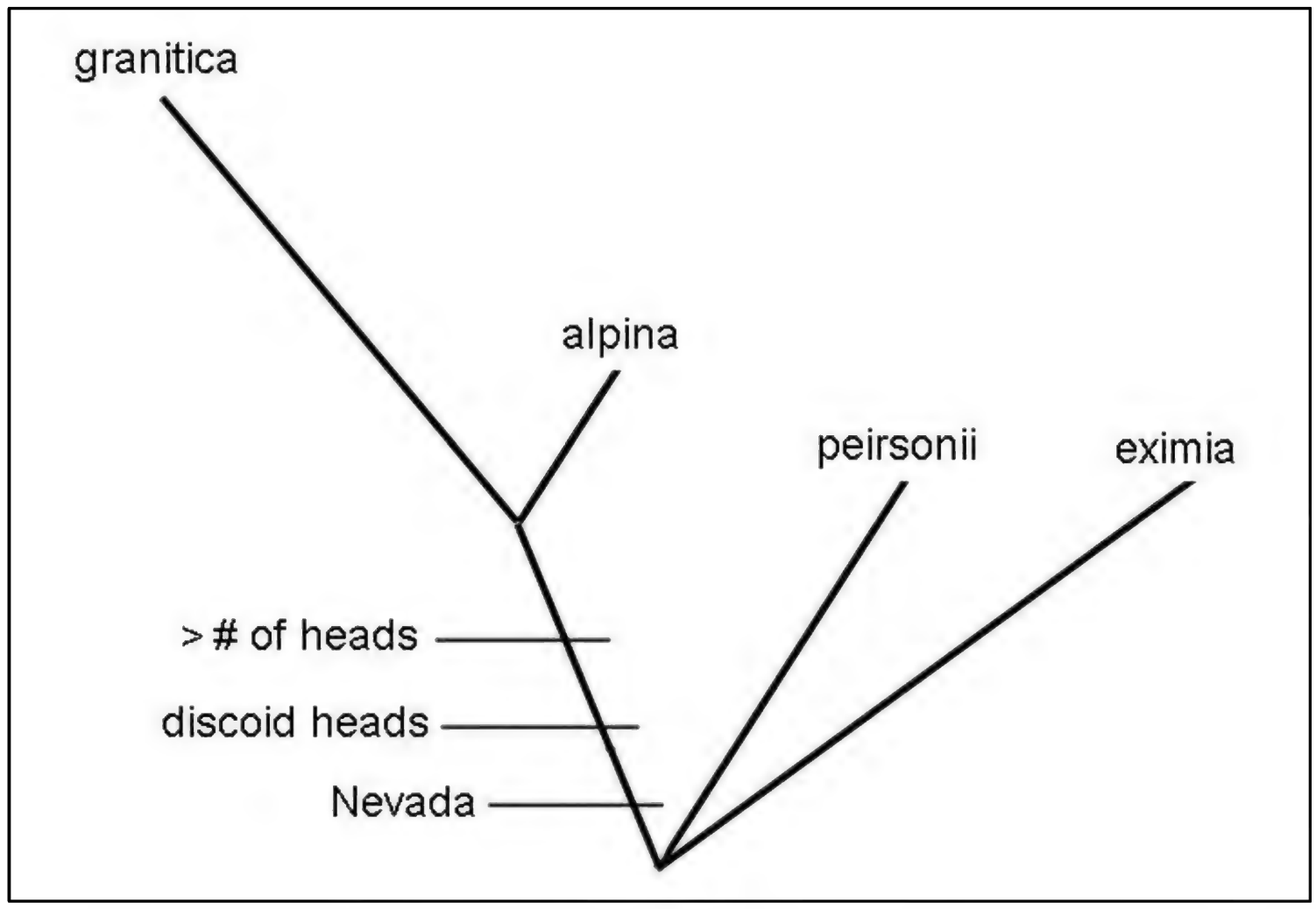

Figure 1. Intuitive phylogeny of *Toiyabea* species. Although *T. granitica* is divergent in morphology (see text and images) from the other three species, it is hypothesized here to share an immediate ancestor with *T. alpina*. Both species have discoid heads, a greater number of heads per stem, and are endemic to isolated mountains in Nevada. If these features were shown to be convergent, then *Toiyabea granitica* might reasonably be treated as a separate genus, perhaps as sister to the others, although a 4-species *Toiyabea* still would be the preferred choice here (see text).

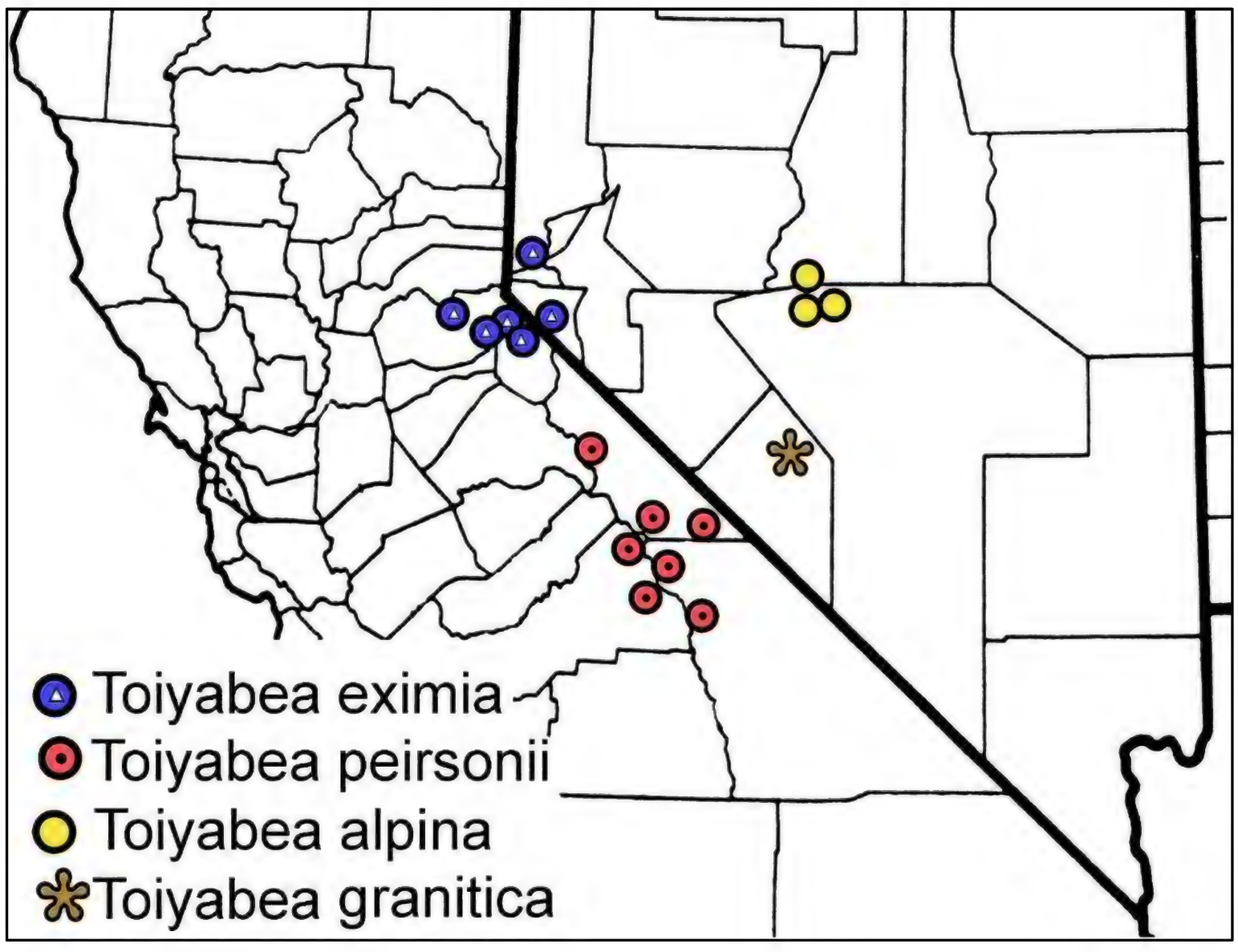

Figure 2. Distribution of *Toiyabea* species.

Figure 3. Vestiture. Top: *Toiyabea granitica*. Bottom: *Toiyabea alpina*.

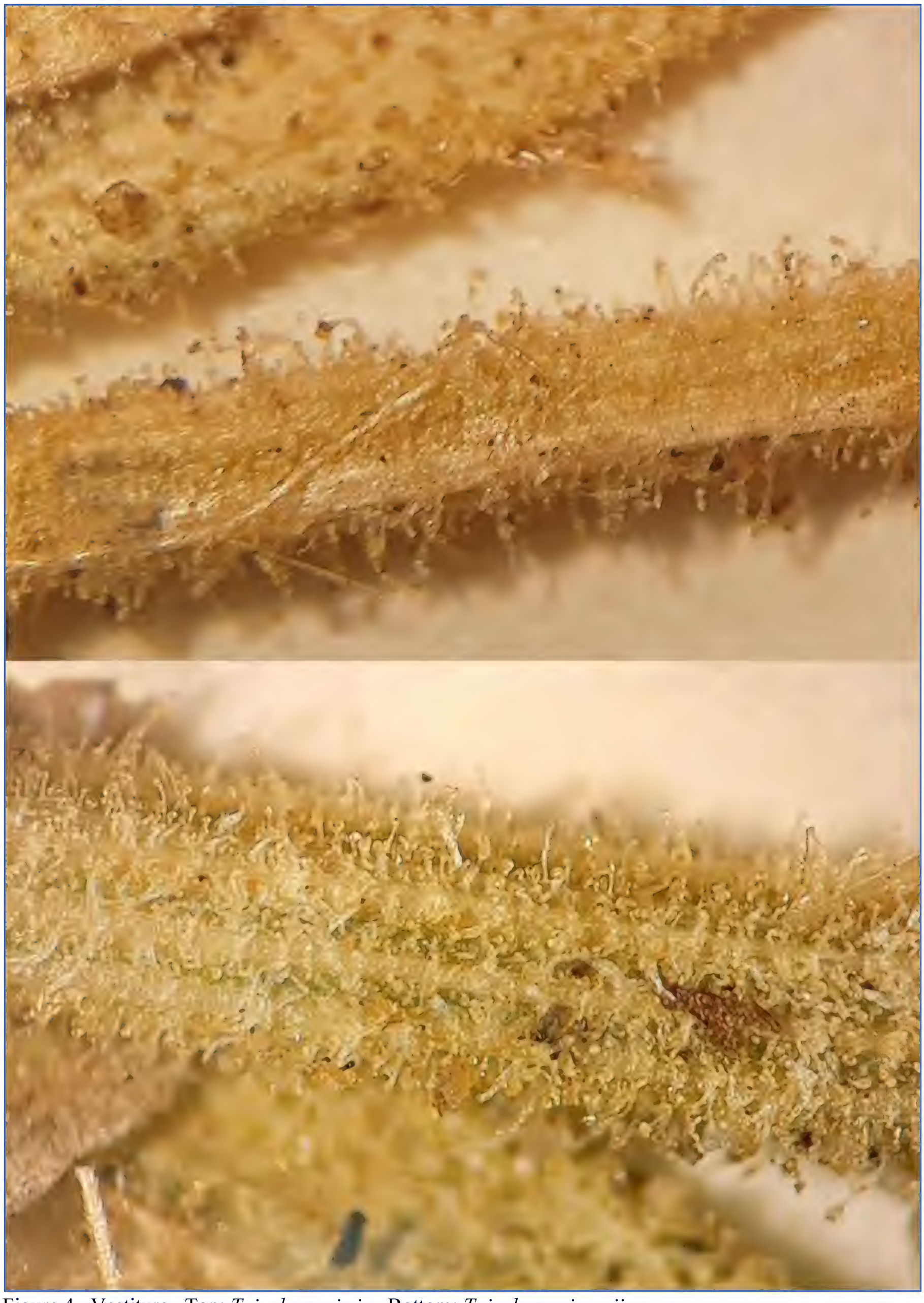

Figure 4. Vestiture. Top: *Toiyabea eximia*. Bottom: *Toiyabea peirsonii*.

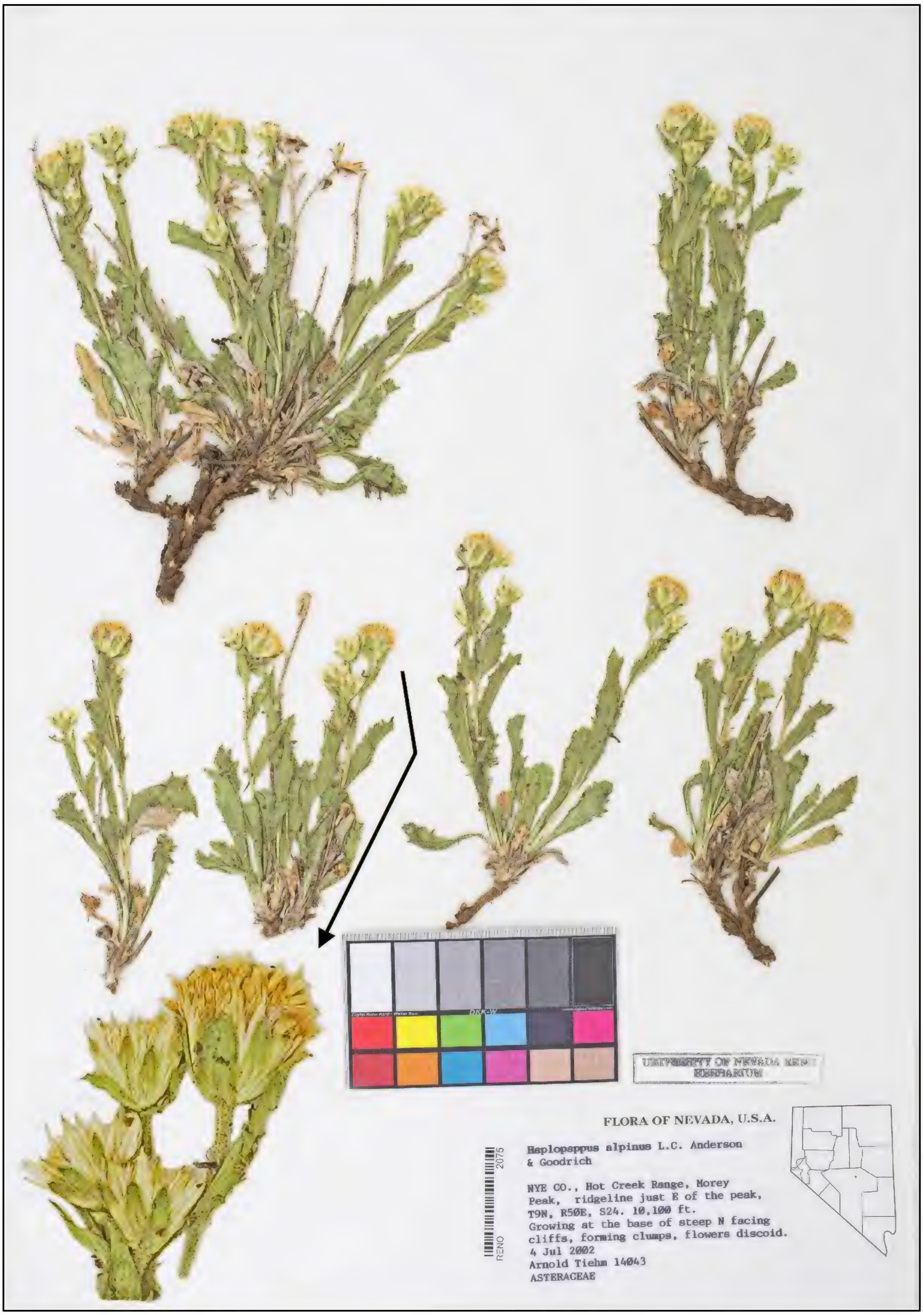

Figure 5. *Toiyabea alpina*, Nye Co., Nevada. *Tiehm 14043* (RENO).

Figure 6. *Toiyabea alpina*, Nye Co., Nevada. From MO isotype.

Figure 7. *Toiyabea alpina*, Nye Co., Nevada. Photos by Michael P. Spellenberg, 3 August 2013.

Figure 8. *Toiyabea granitica*, Esmerelda Co., Nevada. Holotype NY, *Tiehm 8346*.

Figure 9. *Toiyabea granitica*, from the TEX isotype.

Figure 10. *Toiyabea granitica*, isotype WTU.

Figure 11. *Toiyabea granitica*, paratype, *Tiehm 15338* (NY).

Figure 12. *Toiyabea granitica*, from GH isotype.

Figure 13. *Toiyabea granitica*, leaf variation, from the holotype and isotypes.

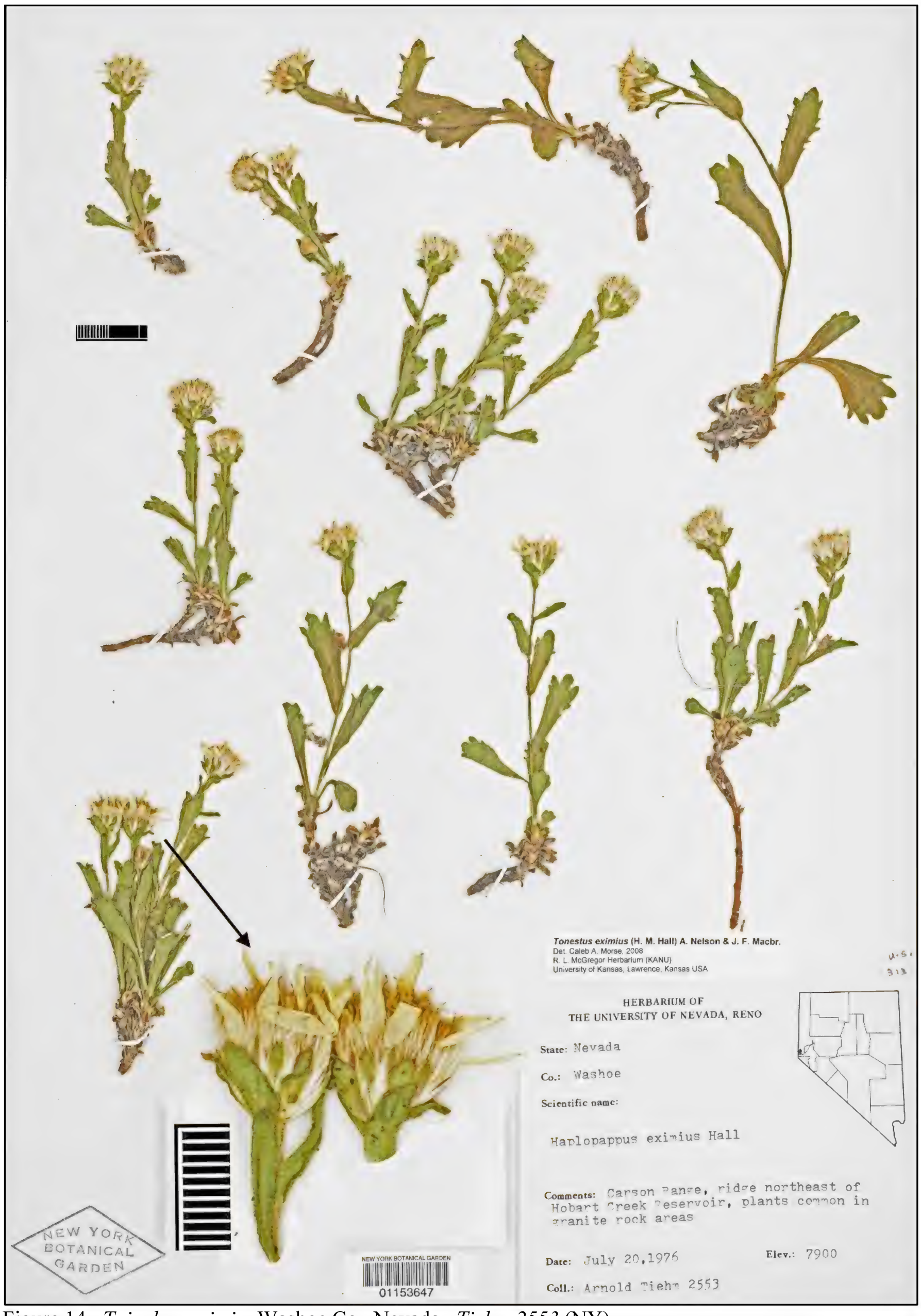

Figure 14. *Toiyabea eximia*, Washoe Co., Nevada. *Tiehm 2553* (NY).

Figure 15. *Toiyabea eximia*, El Dorado Co., California. From GH isotype.

Figure 16. *Toiyabea eximia*. Top: Alpine Co., California. Photo by Steven Sperry, 30 July 2010. Bottom: Washoe Co. Nevada. Photo by Steve Matson, 23 July 2003.

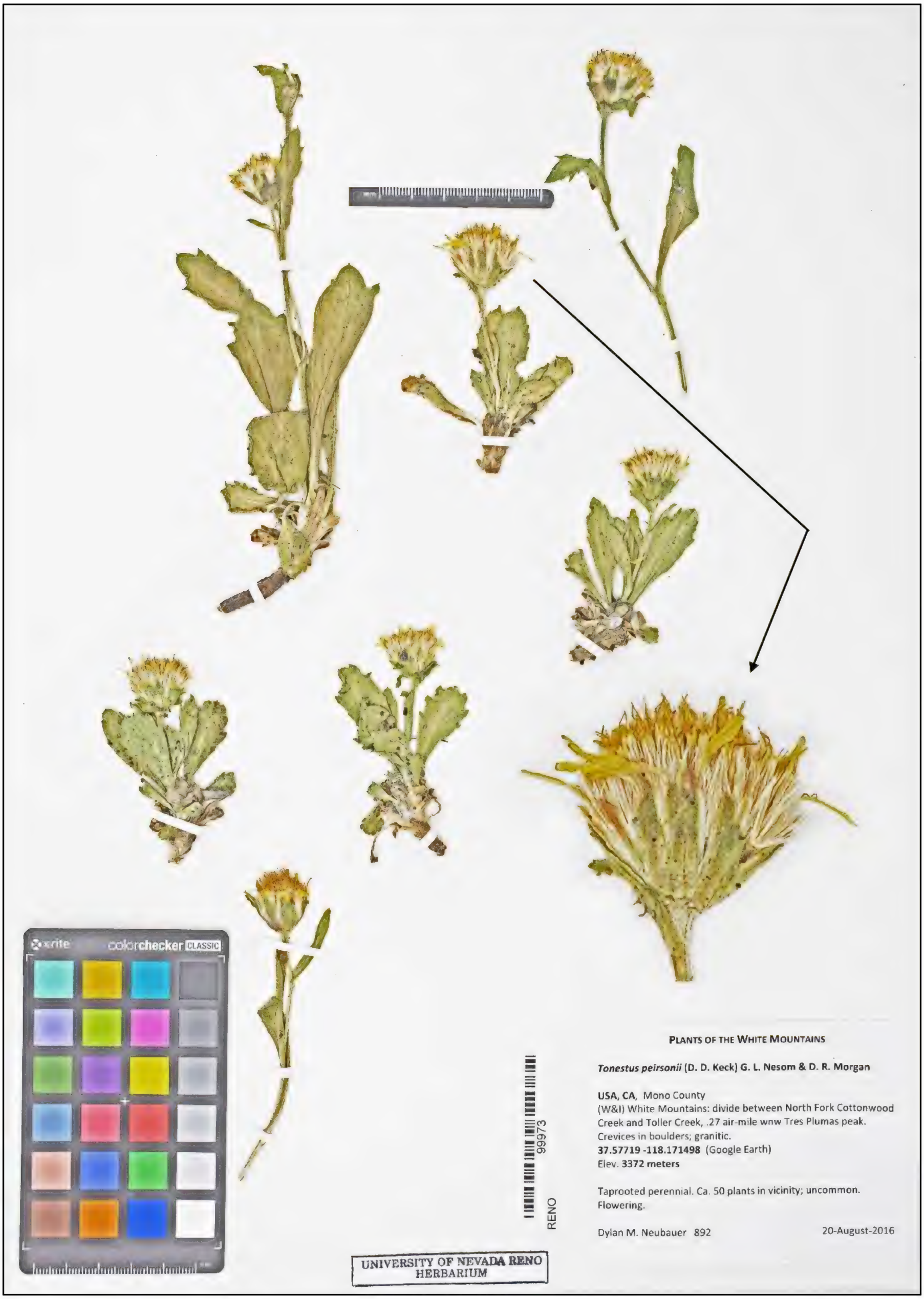

Figure 17. *Toiyabea peirsonii*, Mono Co., California. *Neubauer 892* (RENO).

Figure 18. *Toiyabea peirsonii*, Inyo Co., California. From the holotype.

Figure 19. *Toiyabea peirsonii*, Inyo Co., California. Photo by Morgan Stickrod, 21 August 2018.

Figure 20. *Toiyabea peirsonii*, Inyo Co., California. Photo by Jane S. Richardson, 3 August 2013.

Figure 21. *Toiyabea peirsonii*, Inyo Co., California. Photo by Jane S. Richardson, 3 August 2013.

Figure 22. *Toiyabea peirsonii*, Inyo Co., California. Top: Photo by Steven Sharnoff, no date given. Bottom: Photo by Jane S. Richardson, 3 August 2013.

ACKNOWLEDGEMENTS

Thanks to the staff at PH and NY for hospitality during study there. And I'm grateful for the effort and various sources of funding that have made specimen data and images available through online databases. In situ images by photographers in the field are invaluable.

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SYNOPSIS WITH NEW COMBINATIONS OF *HELIOTROPIUM* (HELIOTROPIACEAE, BORAGINALES) FOR TAXA FROM THE WEST INDIES PREVIOUSLY IN *TOURNEFORTIA*

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ABSTRACT

In the Catalogue of Seed Plants of the West Indies, the genus *Tournefortia* sensu stricto was accepted, but as more data suggest it should be included in *Heliotropium*, it feels useful to provide a list of the additional names in *Heliotropium*. Sixteen species are cited, including nine new combinations and one new name.

Recent papers (Feuillet 2019, 2020) provide new names in *Heliotropium* for *Tournefortia* species in preparation of the Boraginales treatment for Flora of the Guianas and give the reason why this is necessary. A checklist and new combinations are provided here as an addition to the Feuillet treatment (2012) of the Heliotropiaceae in the Catalog of Seed Plants of the West Indies.

1. **Heliotropium astrotrichum** (DC.) Govaerts, Skvortsovia 4: 92. 2018. Basionym: *Tournefortia astrotricha* DC., Prodr. 9: 520. 1845.

1a. **Heliotropium astrotrichum** var. **astrotrichum**

Distribution—Cayman Islands and Jamaica.

1b. **Heliotropium astrotrichum** var. **subglabrum** (Stearn) Govaerts, Skvortsovia 4: 92. 2018. Basionym: *Tournefortia astrotricha* var. *subglabra* Stearn, J. Arnold Arbor. 52: 633. 1971.

Distribution—Cayman Islands and Jamaica.

2. **Heliotropium caribaeum** (Griseb.) Feuillet, **comb. nov.** Basionym: *Tournefortia caribaea* Griseb., Fl. Brit. W. I. 484. 1862.

Distribution—Dominica and Martinique.

3. **Heliotropium cuspidatum** (Kunth) Feuillet, Phytoneuron 2019–63: 1. Basionym: *Tournefortia cuspidata* Kunth in H.B.K., Nov. Gen. Sp. (quarto ed.) 3: 83. 1818.

= *Tournefortia obscura* A. DC., Prodr. 9: 517. 1845.
= *Tournefortia setifera* Urb. & Ekman, Ark. Bot. 22^{a}(17): 94. 1929.

Distribution—West Indies, Central and South America.

4. **Heliotropium filiflorum** (Griseb.) Feuillet, **comb. nov.** Basionym: *Tournefortia filiflora* Griseb., Fl. Brit. W. I. 483. 1862.

   Distribution—West Indies.

5. **Heliotropium foetidissimum** (L.) Feuillet, **comb. nov.** Basionym: *Tournefortia foetidissima* L., Sp. Pl. 141. 1753.

   Distribution—Mexico, Hispaniola, Jamaica, and South America.

6. **Heliotropium funkiae** Feuillet, 2020. Phytoneuron 2020-12: 1. Basionym: *Tournefortia bicolor* Sw., Prodr., 40. 1788. *Tournefortia hirsutissima* f. *bicolor* (Sw.) D.L. Nash, Fl. Veracruz 18: 141. 1981; not *Heliotropium bicolor* Hochst. & Steud. = **Euploca strigosa** (Willd.) Diane & Hilger

   = *Tournefortia alba* Splitgerber ex DeVriese, Nederl. Kruidkund. Arch. 1: 347. 1848. *Heliotropium album* (Splitgerber ex De Vriese) Feuillet, 2019; not *Heliotropium album* St.-Lag., in A. Cariot, Étude Fl., ed. 8, 2: 614 (1889); nom. illeg. for *Heliotropium europaeum* L.

   Distribution—West Indies, Central and South America.

7. **Heliotropium gibberosum** (Urb.) Feuillet, **comb. nov.** Basionym: *Tournefortia gibberosa* Urb., Symb. Antill. 7: 349. 1912.

   Distribution—Dominican Republic.

8. **Heliotropium glabrum** (L.) Feuillet, **comb. nov.** Basionym: *Tournefortia glabra* L., Sp. Pl. 141. 1753.

   Distribution—Mexico, Central America, and West Indies.

9. **Heliotropium gnaphalodes** L. Syst. Nat., ed. 10. 2: 913. 1759. Basionym: *Tournefortia gnaphalodes* (L.) R. Br. ex Roem. & Schult., Syst. Veg. 4: 538. 1819.

   Distribution—USA and West Indies.

10. **Heliotropium laevigatum** (Lam.) Feuillet, **comb. nov.** Basionym: *Tournefortia laevivata* Lam., Tabl. Encycl. 1: 416. 1792. *Tournefortia bicolor* var. *laevigata* M. Gomez, Anales Soc. Esp. Hist. Nat. 19: 256. 1890.

    Distribution—West Indies.

11. **Heliotropium lamarckii** Feuillet, **nom. nov.** Basionym: *Tournefortia scabra* Lam., Tabl. Encycl. 1: 417. 1792; non *Heliotropium scabrum* Retz., Observ. Bot. 2: 8. 1781; non *Heliotropium scabrum* Lehm., Asperif. Nucif. 1: 70. 1818.

    Distribution—Greater Antilles and Virgin Islands (St. Thomas).

12. **Heliotropium roigii** (Britton) Feuillet, **comb. nov.** Basionym: *Tournefortia roigii* Britton, Bull. Torrey Bot. Club 53: 462. 1926.

    Distribution—Cuba.

13. **Heliotropium selleanum** (Urb. & Ekman) Feuillet, **comb. nov.** Basionym: *Tournefortia selleana* Urb. & Ekman, Ark. Bot. 20[a](5): 43. 1926.

    Distribution—Haiti.

14. **Heliotropium smaragdinum** (Proctor) Feuillet, **comb. nov.** Basionym: *Tournefortia smaragdina* Proctor, J. Arnold Arbor. 63: 296. 1982.

    Distribution—Jamaica.

15. **Heliotropium stamineum** (Griseb.) Feuillet, **comb. nov.** Basionym: *Tournefortia staminea* Griseb., Fl. Brit. W. I. 484. 1862.

    Distribution—Jamaica.

16. **Heliotropium verdcourtii** Craven, Blumea 50: 378. 2005. Basionym: *Tournefortia hirsutissima* L., Sp. Pl. 1: 140. 1753.

    Distribution—USA, Mexico, Central America, West Indies, and South America.

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Feuillet, C. 2020. Correction for Feuillet (2019): *Heliotropium funkiae*, a new name for *Heliotropium album* (Splitgerber ex De Vriese) Feuillet (Heliotropiaceae, Boraginales). Phytoneuron 2020-n: 1.

Feuillet, C. 2020. Correction for Feuillet (2019): *Heliotropium funkiae*, a new name for *Heliotropium album* (Splitgerber ex de Vriese) Feuillet (Heliotropiaceae, Boraginales). Phytoneuron 2020-12: 1.

CORRECTION FOR FEUILLET (2019): *HELIOTROPIUM FUNKIAE*, A NEW NAME FOR *HELIOTROPIUM ALBUM* (SPLITGERBER EX DE VRIESE) FEUILLET (HELIOTROPIACEAE, BORAGINALES)

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When transferring four *Tournefortia* species to *Heliotropium* (Feuillet 2019), I coined the new combination *Heliotropium album* (Splitgerber ex De Vriese) Feuillet. Heather Lindon, IPNI editor at the Royal Botanic Gardens, Kew, told me that I overlooked a previous taxon: *Heliotropium album* St.-Lag. I thank her for her message. Such later homonyms are rejected (Art. 53.1, note 2 of the Code: Turland et al. 2018) and therefore I here give a new name to that species.

Heliotropium funkiae Feuillet, **nom. nov.** Basionym: *Tournefortia bicolor* Sw., Prodr., 40. 1788. *Tournefortia hirsutissima* f. *bicolor* (Sw.) D.L. Nash, Fl. Veracruz 18: 141. 1981. **TYPE**: **Jamaica**. *Swartz s.n.* (S [photo!]); not *Heliotropium bicolor* Hochst. & Steud. = **Euploca strigosa** (Willd.) Diane & Hilger

= *Tournefortia alba* Splitgerber ex DeVriese, Nederl. Kruidkund. Arch. 1: 347. 1848. *Heliotropium album* (Splitgerber ex De Vriese) Feuillet. **TYPE**: **Surinam**. *Splitgerber 841* (holotype: L!; isotype: P!). Not *Heliotropium album* St.-Lag., in A. Cariot, Étude Fl., ed. 8, 2: 614 (1889); nom. illeg. for **Heliotropium europaeum** L.

Distribution—West Indies, Central and South America.

Etymology—The epithet honors Vicki Funk (1947–2019), specialist of the Compositae, former president of the IAPT, my former mentor at the Smithsonian Institution. I am missing our early morning discussions very much.

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ALOCASIA MACRORRHIZOS (ARACEAE), *BUXUS SEMPERVIRENS* (BUXACEAE), AND *NOTHOSCORDUM GRACILE* (ALLIACEAE) NEW IN THE ARKANSAS FLORA, WITH ADDITIONAL NOTEWORTHY RECORDS OF ANGIOSPERMS FOR THE STATE

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ABSTRACT

Nothoscordum gracile (Dryander) Stearn is here documented for a first occurrence in the Arkansas flora, outside of cultivation. In 2019, eight escaped plants of *N. gracile* were discovered growing as weeds in a disturbed lawn area along a street edge in the city of Arkadelphia in Clark County, Arkansas. *Alocasia macrorrhizos* (L.) G. Don and *Buxus sempervirens* L. also are documented for first occurrences in Arkansas as adventive waifs. Two spontaneous plants of *A. macrorrhizos* were discovered growing in a large dumpsite for horticultural waste in Clark County in 2018. The *A. macrorrhizos* plants have persisted through 2019. Several plants of *B. sempervirens* were discovered along Mill Creek, adjacent to the Ouachita River, establishing from horticultural discards. The *A. macrorrhizos* and *B. sempervirens* records represent the first documented occurrences of the genera *Alocasia* and *Buxus*, along with the Buxaceae family, in Arkansas, not in cultivation. Additionally, eight species of angiosperms, *Euonymus japonicus* Thunb., *Koelreuteria bipinnata*, *Liriope graminifolia, Liriope muscari*, *Ophiopogon japonicus*, *Physalis philadelphica*, *Trachelospermum jasminoides*, and *Vitex negundo*, are reported for second or third occurrences in the Arkansas flora or as significant county records.

NOTHOSCORDUM GRACILE

In 2019, eight escaped plants of *Nothoscordum gracile* (Dryander) Stearn (fragrant false garlic) were discovered growing at the edge of a street in a highly disturbed lawn area of a residence in the city of Arkadelphia in Clark County (Fig. 1). Propagules, presumably seeds and/or bulblets, apparently were transported via runoff water to the site from cultivated plants of *N. gracile* that occurred upslope from the site, allowing for establishment of the escaped plants. This record represents the first documented occurrence of this species in Arkansas, outside of cultivation.

Nothoscordum gracile is a bulbaceous perennial that is native to the Americas, possibly Argentina (Ravenna 1991; Jacobsen & McNeal 2002). This species has a somewhat convoluted nomenclatural history, with a number of epithets and misapplications, including *N. borbonicum* Kunth, *N. fragrans* (Vent.) Kunth, and *N. inodorum* (Ait.) Nichols. (Ravenna 1991; Jacobsen & McNeal 2002). Ravenna (1991) proposed that its correct name was *N. borbonicum*, a naturally occurring, interspecific hybrid between *N. gracile* Ait. and *N. entrerianum* Ravenna; however, according to Jacobsen and McNeal (2002), rather than *N. borbonicum*, *N. gracile* is the correct name for this species. *Nothoscordum gracile* sometimes is cultivated in the southern USA, including Arkansas, and has become naturalized in a number of other states (Jacobsen & McNeal 2002; Weakley 2015). Because of its prolific ability to establish escaped populations from a combination of seeds and bulblets, *N. gracile* should be expected elsewhere in the state's flora.

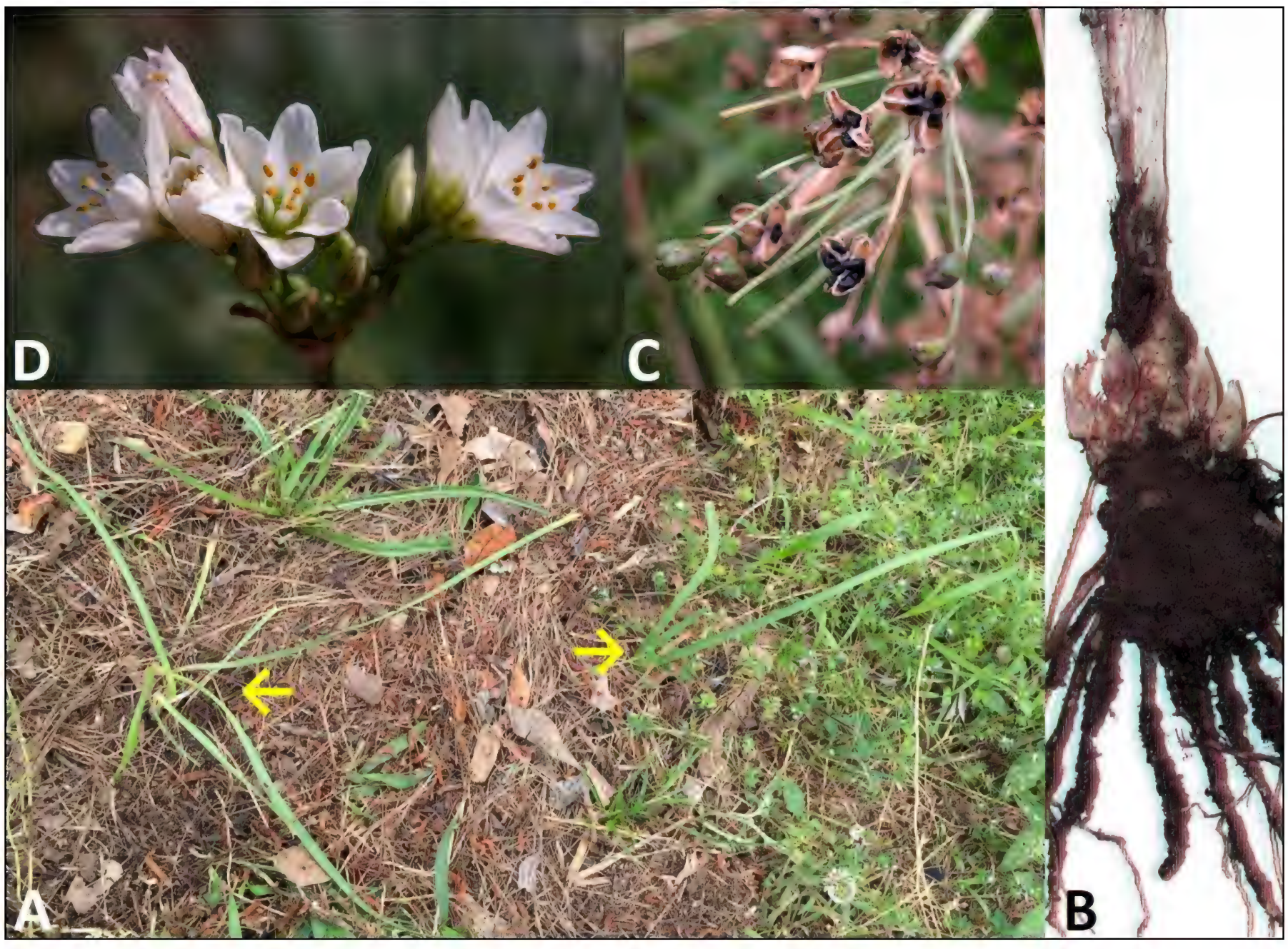

Figure 1. (A–D) *Nothoscordum gracile* escaped in Clark County, Arkansas. (A) Escaped plants at street edge in highly disturbed lawn area; notice plants are small and spaced apart as to indicate probable recent establishment via seeds; two of the plants are designated by yellow-colored arrows. (B) Bulb of escaped plant with numerous bulblets. (C) Mature fruits and seeds. (D) Flowers.

Nothoscordum gracile morphologically is similar to the native *N. bivalve* (L.) Britt. (false garlic, grace garlic) but may be distinguished from it reliably using the following key.

1. Perianth segments united up to one-third of their length; leaves 4–12 mm wide ...**Nothoscordum gracile**
1. Perianth segments separate or only united basally; leaves 1–5 mm wide.....**Nothoscordum bivalve**

Voucher specimen. **Arkansas**. Clark Co.: Small colony of plants growing in highly disturbed lawn area along edge of street — escaped, at intersection of O'Connell St. and 19th St., Arkadelphia, 21 May 2019, *Serviss 8695* (HEND).

ALOCASIA MACRORRHIZOS

In 2018, two spontaneous plants of *Alocasia macrorrhizos* (L.) G. Don (giant taro) were discovered growing at the edge of a dumpsite for horticultural waste in the city of Arkadelphia in Clark County (Fig. 2). The spontaneous plants presumably were established from horticultural discards. *Alocasia macrorrhizos* easily is propagated asexually from tubers and plantlets; hence, discards of these propagules or even whole plants as horticultural waste could have led to their presence at the site. The plants at the dumpsite overwintered from 2018 and were present in 2019. *Alocasia macrorrhizos* sometimes is cultivated in Arkansas and will overwinter (as buried tubers) in at least some years if grown in a protected location. At present, *A. macrorrhizos* should be considered a waif in Arkansas and is not likely to become an established component of the flora. Its presence in Arkansas as spontaneous plants should be expected, however, under conditions similar to those previously described. This record represents the first occurrence of the genus *Alocasia* in the Arkansas flora, not in cultivation.

Figure 2. *Alocasia macrorrhizos* adventive in Clark County, Arkansas — one of two spontaneous plants present at a large dumpsite for horticultural waste in the city of Arkadelphia. Both plants have been present at the site since at least 2018. Several plants of *Rubus* sp. may be seen in the foreground. A number of other non-native species are present at this site, including several escaped plants of *Lagerstroemia indica* L. (crepe myrtle), which appear to have established also from horticultural discards via rooting of stem cuttings.

The only other large-leaved aroid in the Arkansas flora that potentially could be confused with *A. macrorrhizos* is *Colocasia esculenta* (L.) Schott (elephant ear, taro). In addition to much of the *C. esculenta* material naturalized in Arkansas being the aggressively stoloniferous form (see Serviss et al. 2017a — *A. macrorrhizos* is not stoloniferous), the two species also may be distinguished reliably using the following key (some forms of *C. esculenta* are not stoloniferous but are large-bodied and similar to *A. macrorrhizos* in overall form).

1. Veins of adaxial (upper) leaf surface conspicuously raised above the lamina ..... **Alocasia macrorrhizos**
1. Veins of adaxial leaf surface flush with or slightly sunken below the lamina ..... **Colocasia esculenta**

Alocasia macrorrhizos is a tuberous, often caulescent perennial that is native to tropical Asia (Bailey & Bailey 1976). In the USA, it currently has been documented from the naturalized floras of Alabama and Florida (Wunderlin & Hansen 2011; Kartesz 2015; Keener et al. 2019).

Voucher specimens. **Arkansas**. Clark Co.: Two spontaneous plants present at edge of dumpsite for horticultural waste, presumably established from discards, plants have overwintered since at least 2018, W of intersection of Huddleston St. and 12th St., Arkadelphia, 29 Oct 2019, *Serviss 8712* (HEND); Two spontaneous plants present at dumpsite for horticultural waste, presumably established from discards, W of intersection of Huddleston St. and 12th St., Arkadelphia, 26 Oct 2018, *Serviss 8638* (HEND).

BUXUS SEMPERVIRENS

In 2019, two small groups of adventive plants of *Buxus sempervirens* L. (common boxwood) were discovered establishing along the edge of Mill Creek in proximity to where the creek empties into the Ouachita River in Clark County (Fig. 3). The *B. sempervirens* plants appeared to have initially been deposited at the site as horticultural waste consisting of whole plants. Subsequent to deposition, plants survived and establishment continued via adventitious rooting of stems (Fig. 3A). In Arkansas, *B. sempervirens* is planted as a hedge and border plant and as a shade tolerant evergreen. In general, it easily is grown and tolerates regular pruning and shaping, and thus regularly is used in landscaping. At present, it should not be considered an established component of the state's flora; however, it previously has been documented persistent from cultivation in the state (Garland Co., *Serviss 8642*, HEND), and is escaped/naturalized in the floras of a number of other eastern states (Diamond 2013; Kartesz 2015; Keener et al. 2019; USDA, NRCS 2020) — *B. sempervirens* should be expected as escaped elsewhere in Arkansas.

Figure 3. (A–B) *Buxus sempervirens* adventive in Clark County, Arkansas. (A) Stem segment from one of the adventive *B. sempervirens* plants with numerous adventitious roots present. (B) Whole plant established from horticultural discards.

In the Arkansas flora, the small, opposite, leathery leaves, sharply quadrangular stems, and dense growth form of *B. sempervirens* distinguish it from most other shrubs. It potentially could be confused with some of the smaller-leaved, evergreen hollies, such as *Ilex vomitoria* Ait. (yaupon holly) and *I. crenata* Thunb. (Japanese holly) — *I. crenata* is a recent addition to the state's flora; see Serviss et al. 2016c). However, *B. sempervirens* has oppositely arranged leaves, whereas both *Ilex* species have alternate phyllotaxy.

This record represents the first occurrence of the genus *Buxus* and the Buxaceae family in the Arkansas flora, not in cultivation. *Buxus sempervirens* is an evergreen shrub or small tree to eight or more meters tall that is native to Europe, North Africa, and Asia Minor (Bailey & Bailey 1976; Krüssmann 1976). Much natural variation occurs within the species. It has been cultivated for centuries and numerous forms and cultivars currently exist (Krüssmann 1976).

Voucher specimen. **Arkansas**. Clark Co.: Two distinct groups of plants establishing from discarded horticultural waste (whole plants deposited and adventitiously rooting in along stems), edge of Mill Creek at Ouachita River, OBU campus pavilion area, Arkadelphia, 29 Oct 2019, *Serviss 8714* (HEND).

Noteworthy records for Arkansas

EUONYMUS JAPONICUS Thunb. (Japanese spindle tree) is a large, evergreen shrub or small tree to five meters or more that is native to Japan (Bailey & Bailey 1976; Krüssmann 1977; Ma & Funston 2008). It has been reported previously as a component of the naturalized floras of a few eastern states (Diamond 2013; Hannick et al. 2013; Kartesz 2015; Weakley 2015; USDA, NRCS 2020). It first was documented outside of cultivation in Arkansas from Clark County by Serviss et al. (2017b). In 2019, a second naturalized occurrence of *E. japonicus* in Arkansas was documented from Union County (Fig. 4). Two escaped plants of *E. japonicus* occurred along a steep bank of a small stream in an urban greenbelt and riparian zone, with residential areas surrounding the site.

Figure 4. Escaped plants of *Euonymus japonicus* growing on steep streambank in an urban greenbelt in Union County, Arkansas.

Voucher specimen. **Arkansas**. Union Co.: Two escaped plants growing on steep streambank, highly disturbed greenbelt and riparian zone, N/NW of intersection of Briarwood Dr. and Crestwood Dr., El Dorado, 31 Aug 2019, *Serviss 8705* (HEND).

KOELREUTERIA BIPINNATA Franch. (Chinese flame tree) is a small to medium-sized tree to 20 meters that is native to southwestern China (Kriissmann 1977; Xia & Gadek 2007). It occasionally is cultivated in the southern USA for ornamental purposes because of its showy flowers and fruits and its tolerance of a wide variety of soil types (Bailey & Bailey 1976; Krussmann 1977; Griffiths 1992). In addition to Arkansas, *K. bipinnata* has been documented in the naturalized floras of Alabama, Florida, and Georgia (Kartesz 2015). It initially was documented in Arkansas from Clark County in 2005 (Serviss et al. 2006). The site with the original naturalized *K. bipinnata* population was cleared soon following discovery, and the population was believed to be extirpated. However, in 2019, a single, reproductively mature plant was discovered at the site, presumably generated from seeds of previously naturalized plants (Fig. 5). A second, small, naturalized population of *K. bipinnata* in Clark County also is present in close proximity to the site where initially discovered. These three occurrences represent the only known records of this species outside of cultivation in the state. *Koelreuteria bipinnata* prolifically self-seeds, giving rise to large numbers of plants in a short period of time. The species has the potential to be invasive under the correct conditions. It should be expected elsewhere in Arkansas.

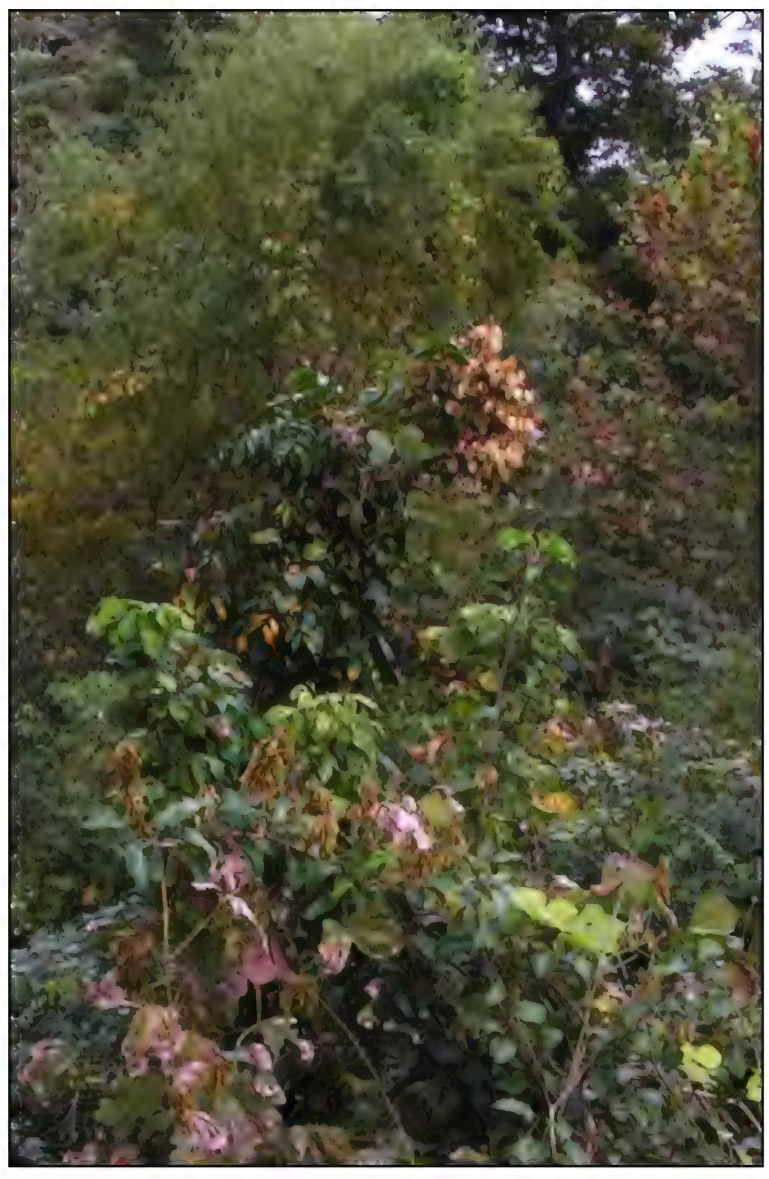

Figure 5. Naturalized plant of *Koelreuteria bipinnata* in Clark County, Arkansas. This plant occurred in a rocky ravine above a small stream in a highly disturbed, urban greenbelt in the city of Arkadelphia. Notice the large infructescence of yellowish-pink, nearly mature fruits (top one-third of photograph).

Voucher specimen. **Arkansas**. Clark Co.: One reproductively mature tree (with nearly mature fruits), ca. four to five meters tall, growing on rocky slope above streambank in ravine and greenbelt, immediately E of University Ave. and N 8th St. intersection, Arkadelphia, 29 Oct 2019, *Serviss 8713* (HEND).

LIRIOPE GRAMINIFOLIA (L.) Baker (grass lilyturf, creeping lilyturf) is a stoloniferous perennial that is native to China, Pakistan, Taiwan, and Vietnam (Chen & Tamura 2000a; Nesom 2010). In the USA, it previously only has been documented outside of cultivation in Arkansas and Texas (Nesom 2010; Serviss et al. 2016b — from Clark and Pulaski counties in Arkansas). In 2019, an additional occurrence of naturalized plants of *L. graminifolia* was documented from Clark County (Fig. 6). Although already known from this county, the record is important because of the few recorded occurrences of this species outside of cultivation in the USA. The *L. graminifolia* plants from 2019 occurred as a small colony of ramets/clones spreading via stoloniferous offsets. Bird-mediated dispersal of seeds from nearby cultivated plants of *L. graminifolia* is the presumed source of the escaped plants.

Figure 6. (A–B) *Liriope graminifolia* escaped in Clark County, Arkansas. (A) Voucher specimen: notice the elongate, slender stolons at the lower left (designated by yellow-colored arrows), wide leaves, and tall inflorescences. (B) Escaped plants in habitat; several ramets/clones may be seen. The colony is slightly larger than what is shown in the photograph.

Voucher specimen. **Arkansas**. Clark Co.: Small colony of escaped plants growing in moist soil in disturbed, overgrown area, plants with flowers, off 10th St. immediately W of University Ave., Arkadelphia, 19 Sep 2019, *Serviss 8710* (HEND).

LIRIOPE MUSCARI (Dcne.) L.H. Bailey (monkey grass) is a caespitose, sometimes weakly stoloniferous perennial that is native to China, Japan, and Taiwan (Chen & Tamura 2000a; Nesom 2010). In addition to Arkansas, it previously has been documented from Alabama, Georgia, Kansas, Louisiana, Maryland, Mississippi, Missouri, North Carolina, South Carolina, and Tennessee (Thomas & Allen 1993; Nesom 2010; Kartesz 2015; Weakley 2015). *Liriope muscari* initially was documented outside of cultivation in Arkansas by Serviss et al. (2016a) from Clark, Garland, and Pulaski counties. In 2019, two additional occurrences of *L. muscari* were recorded from Hot Spring and Union counties. The Hot Spring County plants consisted of a small population of a few closely spaced clumps growing at the edge of a disturbed woods near Prairie Bayou. In Union County, two escaped plants were observed (one growing in the streambed near the water line and a second toward the top of a steep bank) along a small stream in a highly disturbed greenbelt and riparian zone within the city of El Dorado.

Voucher specimens. **Arkansas**. Hot Spring Co.: A few clumps of escaped plants just inside edge of disturbed woods, plants in flower, off Hwy 84, Prairie Bayou, 1–2 miles NE of Junction 128 and Hwy

84 intersection, 3 Aug 2019, *Serviss 8698* (HEND). Union Co.: Two escaped plants: one plant at top of steep streambank and the second plant at edge of streambed near waterline, plants with spent flowers, highly disturbed, urban greenbelt and riparian zone, N/NW of intersection of Briarwood Dr. and Crestwood Dr., El Dorado, 31 Aug 2019, *Serviss 8704* (HEND).

OPHIOPOGON JAPONICUS (L.f.) Ker-Gawl. (Japanese mondo grass) is a stoloniferous perennial that is native to China, Japan, Korea, and Taiwan (Chen & Tamura 2000b; Nesom 2010). In addition to Arkansas, it only has been documented outside of cultivation in four states: Alabama, Mississippi, North Carolina, and Texas (Diggs et al. 1999; Nesom 2010; Spaulding et al. 2010; Roling et al. 2011; Weakley 2015). It first was documented in the Arkansas flora by Serviss et al. (2016a) from Clark and Pulaski counties. In 2016 and 2019, naturalized populations of *O. japonicus* were recorded from Garland and Union counties, respectively. The Garland County plants were spreading in an unkempt lawn area of an old homesite, presumably naturalizing mostly or exclusively via stoloniferous offsets. The Union County plants occurred as a single, large population along the top of a steep streambank in a highly disturbed, urban greenbelt and riparian zone.

Voucher specimens. **Arkansas**. Garland Co.: Several plants/ramets naturalized at old homesite in disturbed woods, plants reproductive with young fruits/seeds, Conway Terr., 3431.895N, -9302.53W, Hot Springs, 7 Sep 2016, *Olsen 7* (HEND); Colony of hundreds of plants/ramets, escaped from cultivation, wooded area of residence, Conway Terr., Hollywood Estate, Hot Springs, 30 Aug 2016, *Olsen 6* (HEND). Union Co.: Colony of hundreds of clones/ramets growing on top and side of steep streambank of highly disturbed, urban greenbelt and riparian zone, N/NW of intersection of Briarwood Dr. and Crestwood Dr., El Dorado, 31 Aug 2019, *Serviss 8702* (HEND).

PHYSALIS PHILADELPHICA Lam. (tomatillo, Mexican ground cherry) is an annual herb to 1.3 meters tall that is native to Mexico (Bailey & Bailey 1976). It is naturalized in a number of states (Kartesz 2015; USDA, NRCS 2020). This species is the tomatillo of commerce, the fruits of which are used in Latin American cuisine. In 2018, one to two large plants of *P. philadelphica* were discovered growing on the rocky bank of Hot Springs Creek in Garland County, in immediate proximity to a sewer access point (Fig. 7). Plants had flowers and mature fruits. The fruits resembled typical tomatillos in color and size, with some having a diameter of over seven centimeters (Fig. 7A). Seeds distributed to the site by stream or waste water presumably gave rise to the plants. *Physalis philadelphica* previously only has been documented in Arkansas from Craighead County (Gentry et al. 2013).

Voucher specimen. **Arkansas**. Garland Co.: One to two spontaneous plants growing on rocky streambank of Hot Springs Creek, adjacent to sewer manhole access area, plants with flowers and mature fruits, probably established via seeds from sewer overflow, adjacent to intersection of Fontana Rd. and Tatum St., 50 meters N of Fontana Rd., 34.0465691, -93.042161, Hot Springs, 13 Jul 2018, *Serviss 8616* (HEND).

TRACHELOSPERMUM JASMINOIDES (Lindl.) Lem. (Confederate jasmine) is an aggressive, twining, evergreen liana to 10 meters that is native to China (Bailey & Bailey 1976; Li et al. 1995). In addition to Arkansas, it has been documented outside of cultivation in a number of southern states, including Alabama, Arizona, Florida, Georgia, Louisiana, and Texas (Kartesz 2015; USDA, NRCS 2020). *Trachelospermum jasminoides* previously has been documented in Arkansas from Clark and Drew counties (Gentry et al. 2013; Serviss et al. 2015). In 2019, it was recorded from Union County growing along a steep streambank in a highly disturbed greenbelt and riparian zone (Fig. 8). Plants also were observed climbing trees. Naturalized plants of *T. jasminoides* also were recorded from Clark County in 2017 (subsequent to the 2015 record), with plants exhibiting similar patterns of growth and establishment to that observed with those in 2015. *Trachelospermum jasminoides* likely is more widespread in Arkansas than current records indicate, and it appears to have a high potential for invasiveness.

Figure 7. (A–B) *Physalis philadelphica* escaped in Garland County, Arkansas. (A) Voucher specimen of escaped plant of *P. philadelphica*; it occurred along a highly disturbed, open, rocky area of the streambank. One to two reproductively mature plants of *P. philadelphica* were present at the site, along with numerous plants of *Lycopersicum esculentum* Mill. (tomato) and *Cucurbita pepo* L. (squash). (B) Habitat showing escaped *Physalis* and *Lycopersicum* plants. A large, sewer access manhole is present just to the right of the area shown in the photograph.

Figure 8. Naturalized plants of *Trachelospermum jasminoides* in Union County, Arkansas. Plants cover the nearly vertical bank, extending considerably beyond what is shown in the photograph. Plants occurred from the waterline to the top of the bank and also were climbing nearby trees.

In Arkansas, *Trachelospermum jasminoides* closely resembles the native *Thyrsanthella difformе* (Walt.) Pichon (climbing dogbane) and *Gelsemium sempervirens* (L.) St. Hill (yellow jasmine); however, *T. jasminoides* may be distinguished from these species reliably using the following key.

1. Plant exudes milky-white sap when damaged or cut; stems pubescent, at least when young; flowers white to cream or pale yellow in color; fruit an elongate, linear follicle, many times longer than wide.

2. Leaves coriaceous and often with conspicuous pale-green to whitish-green venation on the upper surface; corolla lobes ca. 8 mm long or longer ..... **Trachelospermum jasminoides**
2. Leaves membranous to subcoriaceous and without conspicuously pale-green or whitish-green venation on the upper surface; corolla lobes 5 mm or less long..... **Thyrsanthella difformе**

1. Plant without milky-white sap; stems glabrous; flowers bright yellow; fruit a rounded to ellipsoid capsule, about as long as wide ..... **Gelsemium sempervirens**

Voucher specimens. **Arkansas**. Clark Co.: Plants spreading along the ground at edge of roadside, escaped, disturbed roadside adjacent to homesite, on Deceiper Hill Rd., immediately SW of intersection of Hwy 26 and Deceiper Hill Rd., 28 Sep 2017, *Serviss 8601A1* (HEND); Many plants covering the ground and climbing into trees, semi-wooded waste area of residential zone, Elaine Circle, W/SW of intersection of Elaine Circle and 21st St., Arkadelphia, 1 Sep 2017, *Serviss 8582* (HEND). Union Co.: Large expanse of plants covering the streambank and climbing into trees, naturalized, highly disturbed, urban greenbelt and riparian zone, N/NW of intersection of Briarwood Dr. and Crestwood Dr., El Dorado, 31 Aug 2019, *Serviss 8706* (HEND).

Figure 9. Escaped plants of *Vitex negundo* in Clark County, Arkansas. Plants occurred in a highly disturbed, mostly open area at the edge of the road. A second, smaller plant of *V. negundo* may be seen a short distance behind the one in flower. No other plants of *V. negundo* were apparent in the vicinity.

VITEX NEGUNDO L. (negundo chaste tree) is a large, deciduous shrub or small tree to a height of eight or nine meters that is native to Europe, Asia, and possibly portions of North Africa (Bailey & Bailey 1976; Kriissmann 1978). In addition to Arkansas, *V. negundo* has been documented from the naturalized floras of Alabama, Florida, Louisiana, Maryland, Missouri, Ohio, Oklahoma, and Texas (Kartesz 2015; USDA. NRCS 2020). It previously was documented in Arkansas from Baxter, Drew, Garland, Lincoln, Miller, Pulaski, and Yell counties (Serviss et al. 2007; Gentry et al. 2013). In 2019, two escaped plants of *V. negundo* were discovered growing along a roadside in Clark County (Fig. 9); no other plants of *V. negundo* were observed in the vicinity. Documentation of *V. negundo* from new counties is important because of its tendency to establish naturalized populations via prolific self-seeding.

Voucher specimen. **Arkansas**. Clark Co.: Two escaped plants, larger one ca. 1.3 meters tall and in flower, growing along roadside next to shoulder; no other plants of *V. negundo* observed in the vicinity, at 99 Serenity Ln., Arkadelphia area just W of the main city, 28 Sep 2019, *Serviss 8711* (HEND).

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UNA ESPECIE NUEVA DE *CROTALARIA* (LEGUMINOSAE, PAPILIONOIDEAE) PARA MÉXICO

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RESUMEN

Se describe e ilustra a **Crotalaria lidiae** Ramírez–Hernández & Cruz Durán, **sp. nov**. (Leguminosae, Papilionoideae), una especie nueva de la vertiente del Pacífico mexicano. Es afín a **C. cajanifolia** Kunth, sin embargo se distingue de esta última por ser subarbustos hasta 2 m de alto y presentar inflorescencias con la parte apical capituliforme, con flores en botón ascendentes y con ápice fuertemente curvado, cáliz con lóbulos lanceolar–subulados, con los lóbulos laterales fusionados en la parte apical, brácteas lanceoladas a subuladas, persistentes, estandarte más largo y distribución en la vertiente del Pacífico mexicano.

ABSTRACT

Crotalaria lidiae Ramírez–Hernández & Cruz–Durán **sp. nov.** (Leguminosae, Papilionoideae), a new species from the Mexican Pacific slope, is described and illustrated. It is similar to *C. cajanifolia* Kunth but distinguished by being a subshrub up to 2 m high, with inflorescences with a capituliform apical part, flower buds ascending and with a strongly curved apex, calyx lobes lanceolate–subulate, the laterals fused at the apex, bracts lanceolate to subulate, standard longer, and a distribution restricted to the Pacific slope of Guerrero and Oaxaca.

El género *Crotalaria* L. se caracteriza por presentar flores amarillas, cáliz lobulado, quilla con espolón prominente, androceo monadelfo y legumbres infladas (Bernal 1986). Sus números cromosómicos más frecuentes son 2n=16, 32 y los menos corresponden a especies con 2n=14 (Aldama et al. 2006). Es un género tropical y subtropical con la mayor concentración de sus especies en el hemisferio sur, específicamente en África y Madagascar. A nivel mundial está conformado por 690 especies, de las cuales 90 se registran en América (Fabbroni & Lozano 2013). En el continente americano, su distribución va del sur de Estados Unidos hasta Argentina subtropical y Uruguay (Windler 1974); en México se han registrado 21 especies, 8 de ellas endémicas (Soto 2004).

Como parte de la revisión taxonómica del género *Crotalaria* para el estado de Guerrero, México (Ramírez, 2015), donde se registran 14 especies y dos variedades, también se detectaron ejemplares botánicos que no concuerdan con alguna de las especies hasta ahora conocidas del género. Los ejemplares señalados habían sido previamente confundidos con *C. cajanifolia* Kunth y *C. micans* Link. Sin embargo, el nuevo taxón es distinto en caracteres florares y vegetativos. En la revisión taxonómica antes mencionada, se postuló que la nueva entidad podría distribuirse no sólo en los estados de Guerrero y Oaxaca, sino muy posiblemente en otros estados de la vertiente del Pacífico mexicano, tentativamente desde Michoacán hasta Sinaloa. De esta forma, se examinaron todas las colectas de la región del Pacífico mexicano depositadas en el Herbarios Nacional de México (MEXU), Herbario de la Facultad de Ciencias (FCME) y Herbario de la Escuela Nacional de Ciencias Biológicas (ENCB). Además, se revisaron los tratamientos taxonómicos para *Crotalaria* en Flora Novo–Galiciana (McVaugh 1987) y Flora del Valle de Tehuacán–Cuicatlán (Soto 2004). Así, se propone como especie nueva.

CROTALARIA LIDIAE Ramírez–Hernández & Cruz Durán, **sp. nov**. **TIPO**: **MÉXICO**. **Guerrero**: Mpio. Chilpancingo: Rincón de la Vía, 30 agosto 1959, *H. Kruse 9* (holotipo: MEXU!; isotipo: FCME!). Figura 1.

Subshrub or subfruticose herbs up to 2 m high, inflorescences with more than 100 flowers, open flowers and bracts crowded at the apex, flower buds ascending and with a strongly curved apex, calyx lobes lanceolate–subulate, lateral lobes fused at the apex, the lower lobe reaching in length the medial part of the keel curvature, bracts persistent and lanceolate to subulate, standard 12−14 mm, keel apex up to 4.9 mm long, distributed on the Mexican Pacific slope.

Subarbustos o **hierbas** sufruticosas (0.4–)0.8–2 m de alto, erectas; tallos levemente seríceos. **Hojas** 7.7–14.6 cm de largo, trifolioladas; estípulas 1–2.2 mm de largo, filiformes, seríceas, persistentes; pecíolos (2.8–)3.5–5(–6.2) cm de largo, seríceos; folíolos (3.8–)4.8–8.4 × (1.4–)2–3.4 cm, elípticos a lanceolados, el haz glabro con pubescencia en la vena media, el envés seríceo, la base atenuada a cuneada, el margen ciliado, el ápice apiculado a cuspidado, mucronado. **Inflorescencias** en racimos opositifolios, con 20 a más de 100 flores, las flores aglomeradas y compactas hacia la parte terminal, las brácteas forman un penacho terminal debido al apiñamiento de las flores en conjunto con las brácteas, dándole la apariencia de "capítulo", las flores en botón son ascendentes y presentan ápice fuertemente incurvado; pedúnculo 1.6–3.6 cm de largo; raquis 9.7–29 cm de largo, seríceo; brácteas (4.5–)6–12(–15) mm de largo, lanceoladas a subuladas, seríceas, persistentes; pedicelos 5.6 – 6.6 mm de largo, generalmente igual o más cortos que las brácteas; bractéolas 0.8–1.2 mm de largo, en la parte media y alta del pedicelo, filiformes, seríceas, deciduas; una vez que las flores caducan, las zonas de donde se desprende el pedicelo se conservan a momo de protuberancias que se continúan de modo decurrente en el raquis. **Flores** con corola amarilla; cáliz 7–13 mm de largo, pardo, seríceo, trunco en la base, los lóbulos 6.4–11 mm de largo, lanceolado–subulados, el lóbulo central es libre y alcanza en longitud la parte media de la curvatura de la quilla, los lóbulos laterales generalmente unidos a nivel del ápice; estandarte 12–14 × 11–12 mm, cordiforme, adaxialmente con un par de apéndices engrosados y lanosos entre la base de la lámina y la uña, abaxialmente ciliado en la vena media y el ápice, la uña 3 × 3.6 mm, pubescente; alas 8–10 × 3.3–4 mm, subtriangulares, más cortas que la quilla, con filas de dobleces entre las venas superiores, presentando cilios en el margen carinal, uñas 3.5 × 0.9 mm con los márgenes ciliados; quilla 12–13 × 7 mm, curva, más larga que las alas, los márgenes abaxial y adaxial ciliados, el ápice (2.5–)3–4.1(–4.9) mm de largo, prolongado, curvo, no torcido y con puntos negros, las uñas 2.8–3 × 1–1.4 mm con los márgenes ciliados; androceo 13−16 mm de largo, parte libre de filamentos 5−7 mm de largo, anteras 1–3.3 mm de largo, dimorfas; pistilo con ovario 4 mm de largo, levemente estipitado, pubescente, estilo 12–14 mm de largo, curvo, densamente barbado en el último tercio del lado carinal y vexilar, estigma con el margen barbado. **Legumbres** 2.1–2.4 × 0.8–1 cm, las valvas amarillas a pardo–oscuras en la madurez, seríceas, pico 6–7.4 mm de largo, persistente, el cáliz persistente con los lóbulos laterales fusionados en el ápice. **Semillas** maduras registradas.

Etimología. Esta especie honra la memoria de la C. Lidia Hernández Hernández† (1956–2013), quien fuera una persona ejemplar y madre del primer autor.

Nombre común. Chipile de caballo (Guerrero), chepil de caballo (Oaxaca). En el estado de Guerrero tiene uso forrajero.

Ejemplares adicionales examinados. MÉXICO. **Guerrero.** Mpio. Acapulco de Juárez, La Hacienda, Ejido El Podrido, *Gil 31* (FCME; MEXU); Parque Nacional El Veladero, *Noriega 689* (FCME); El Veladero, *Hernández 56* (FCME). Mpio. Atoyac de Álvarez; 2 km del Salto, *Turrubiarte 222* (FCME); Isla Zacoalpan, Laguna de Mitla, *Lozada 137* (FCME). Mpio. Ayutla de los Libres, 22 km de Ayutla, rumbo a Pascala del Oro, *Velázquez 673* (FCME). Mpio. Chilpancingo de los Bravo, Rincón de La Vía, *Kruse 574* (FCME, MEXU); 1 km al NO del Rincón de La Vía, *Verduzco 127* (FCME); Acahuizotla, *López 12536* (FCME); Acahuizotla, *R. & A. 217* (FCME); Bienes comunales de Dos Caminos, *Carreto 1463* (FCME); Cerro El Naranjo, *Ramírez 216* (FCME); El Rincón de La Vía, *Dios 13034* (FCME). Mpio. Juan R. Escudero, El Puente, *Carreto 1491* (FCME); Tierra Colorada, a 3 km al S de Acahuizotla, hacia la planta

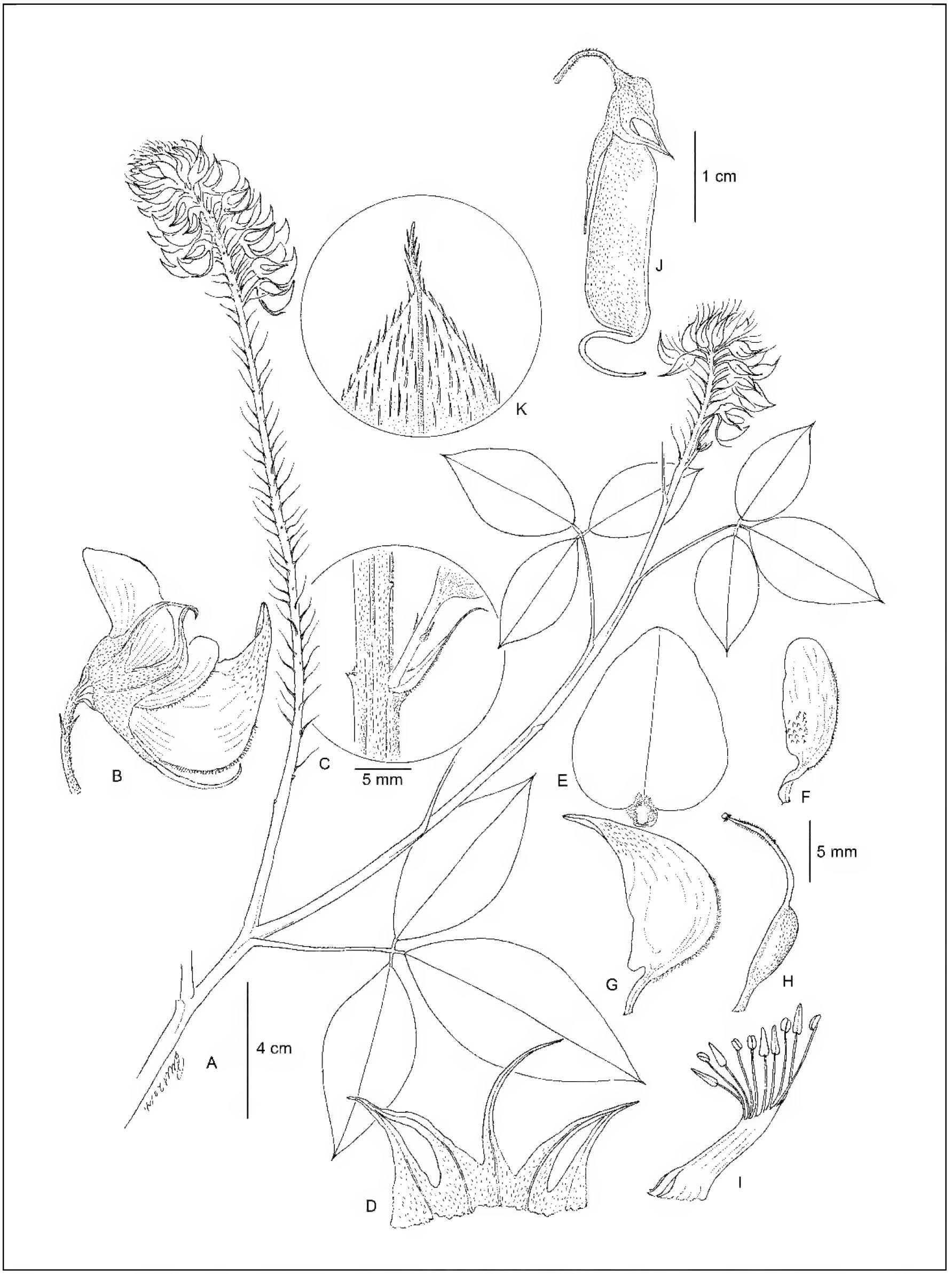
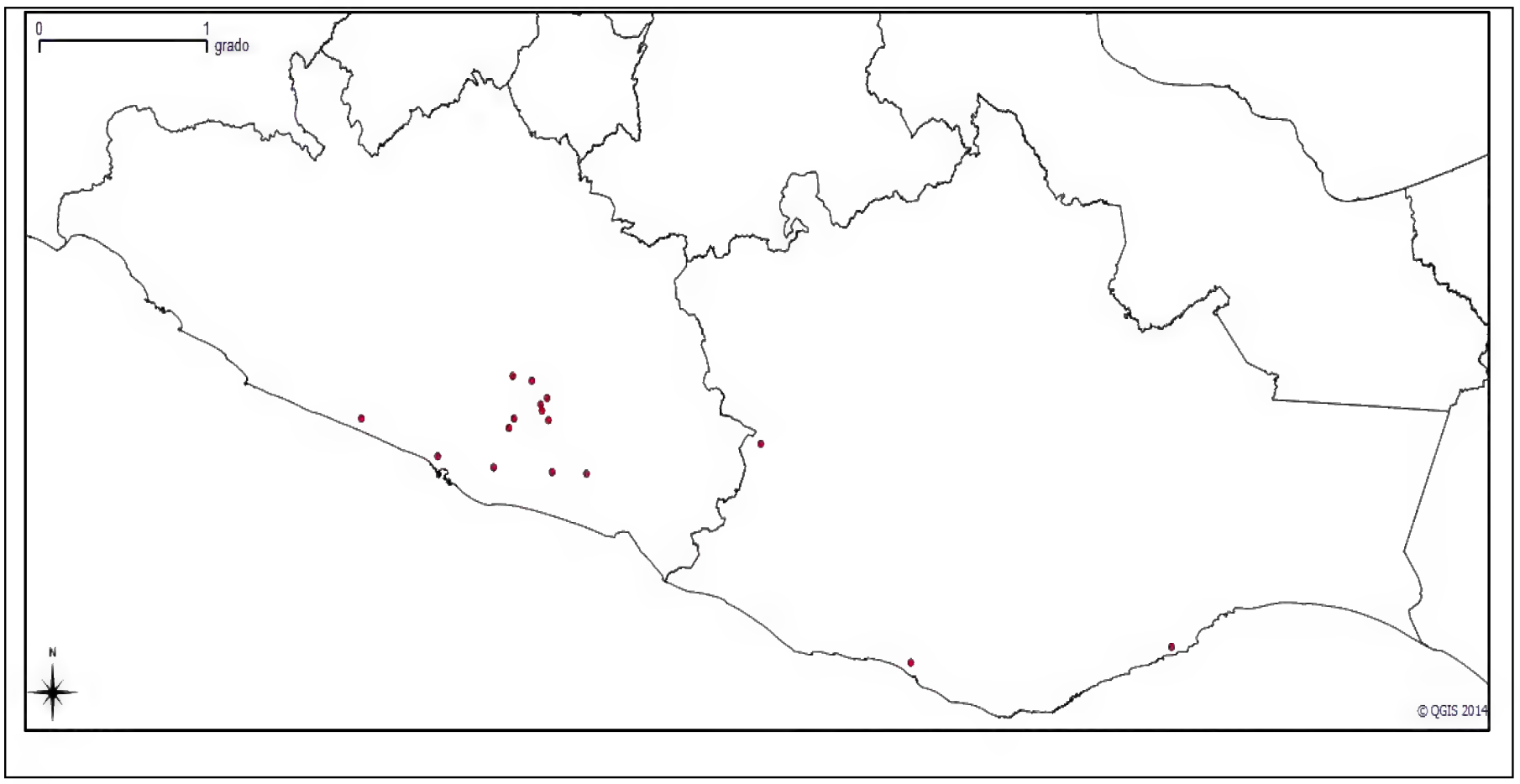


Figura 1. *Crotalaria lidiae* Ramírez–Hernández & Cruz–Durán. A. Rama con inflorescencias. B. Flor. C. Bráctea, pedicelo y bractéola. D. Cáliz. E. Estandarte. F. Ala. G. Quilla. H. Gineceo. I. Androceo. J. Fruto. K. Ápice del folíolo. (A, tomado de *Velázquez 673,* FCME; B−I, tomados de *S.C. 74,* FCME; J, tomado de *Fonseca 1585,* FCME; K, tomado de *Noriega 689,* FCME). Ilustración por Ramiro Cruz Durán.

eléctrica, *Almazán s.n.* (FCME); Tierra Colorada, a 6 km de Tierra Colorada–Ayutla, *Diego 2104* (FCME). Mpio. Mochitlán, Agua de Obispo, *Espinosa 30* (FCME); Agua de Obispo, sobre carretera Chilpancingo-Tierra Colorada, *Núñez 805* (FCME); Agua de Obispo, *s.c. 74* (FCME). Mpio. San Marcos, 7 km delante de Huajintepec, rumbo a Agua Zarca, *Fonseca 1256* (FCME); Río El Cortés, cerca de la carretera Acapulco–Pinotepa, *Fonseca 1885* (FCME). Mpio. Tixtla de Guerrero, 9 km de Chilpancingo a Tixtla, *Diego & de Santiago 9418* (FCME). **OAXACA.** Mpio. Putla Villa de Guerrero, a 2–3 km al S de Mesones, a 28 km al S de Putla, *Sousa 5860* (MEXU). Mpio. San Pedro Mixtepec, 3 millas al N de San Pedro, 15 millas al N de Puerto Escondido, sobre la carretera a Oaxaca, *Lavin 5331* (MEXU). Mpio. Santiago Astata, Barra de la Cruz, 0.5 km al NO, sobre Río Chacalapa, *Elorsa 3679* (MEXU).

Distribución, hábitat y fenología. Se conoce hasta ahora sólo en la vertiente del Pacífico mexicano (Guerrero y Oaxaca). Habita en bosque tropical caducifolio y bosque de pino–encino, o acahuales, en altitudes de 5 a 920(–1400) m. Se ha registrado su asociación con *Ficus* sp., *Salix* sp., *Ludwigia* sp. y Orquidaceae; crece en suelos pedregosos, profundos, con sustrato calizo, arenosos o arcillosos de coloración café claro a oscuro. Florece de (junio–) agosto a octubre y rara vez en febrero–marzo y fructifica de septiembre a octubre y escasamente en febrero.



Mapa 1. Distribución geográfica de *Crotalaria lidiae* en la República Mexicana (estados de Guerrero y Oaxaca).

Afinidades. *Crotalaria cajanifolia* Kunth es la especie que presenta una mayor afinidad taxonómica con *C. lidiae*, sin embargo, es posible distinguirlas tanto por caracteres vegetativos como reproductivos (Cuadro 1). Es importante destacar que *C. lidiae* tiene inflorescencias que en la parte terminal presentan apiñamiento de las flores en botón y que junto con las brácteas semejan un "capítulo", asimismo la flores en botón tiene ápice fuertemente incurvado y tienen posición ascendente. En flores maduras, el lóbulo inferior del cáliz es libre y alcanza en longitud la parte media de la curvatura de la quilla, de igual forma, los lóbulos laterales se fusión en el ápice. Por otro lado, *C. cajanifolia* presenta inflorescencias con la parte terminal a modo de espiga (debido al apiñamiento de las flores), las flores en botón presentan el ápice recto, y las flores son reflejas; en flores maduras, el lóbulo inferior del cáliz no alcanza en longitud la curvatura de laquilla y los lóbulos laterales generalmente son libres (Figuras 1 y 2).

Otra diferencia entre ambas especies radica en sus patrones de distribución: *C. cajanifolia* se distribuye del norte de México hasta Panamá, mientras que *C. lidiae* sólo se ha localizado en la costa del Pacífico mexicano (Mapa 1), hasta el momento en los estados de Guerrero y Oaxaca.

Estructura	*C. lidiae*	*C. cajanifolia*
Tallos		
Pubescencia	levemente serícea	estrigosa a serícea
Folíolos		
Ápice	apiculado a cuspidado, mucronado	agudo a obtuso, mucronado
Inflorescencia		
Brácteas	igual o más largas que los pedicelos, hasta 15 mm de largo,	más cortas que los pedicelos,
Número de flores	20 a más de 100,	20–70,
Distribución floral	aglomerada y compacta hacia la parte superior con apariencia de "capítulo"	aglomerada hacia la partes superior a modo de "espiga"
Flores en botón		
Ápice	fuertemente incurvado,	recto,
Posición	ascendentes	reflejas
Estandarte		
Longitud (mm)	12–14	hasta 10
Cáliz		
Color	pardo,	verdoso,
Lóbulos, longitud (mm)	6.4–11,	4.3–6,
Lóbulos laterales	generalmente unidos en el ápice,	generalmente libres en el ápice,
Lóbulo inferior	alcanza en longitud la parte media de la curvatura de la quilla	no alcanza en longitud la parte media de la curvatura de la quilla
Quilla		
Ápice, longitud (mm)	(2.5–)3–4.1(–4.9)	1.3–2.3
Pistilo		
Estilo	densamente barbado en el lado vexilar y carinal	levemente barbado en el lado vexilar y densamente barbado en el lado carinal
Legumbre		
Pico, longitud (mm)	6–7.4, persistente	generalmente deciduo

Cuadro 1. Comparación morfológica entre *Crotalaria lidiae* y *C. cajanifolia*.

Ejemplares consultados de *Crotalaria cajanifolia*. MÉXICO. Guerrero. Mpio. Atenango del Río, Tuzantlán 2.31 km al NO, *Cruz 6519* (FCME); Apanguito, 2.73 km al NO, *Cruz 5770* (FCME). Mpio. Atoyac de Álvarez, 1 km antes de San Andrés de la Cruz, carretera Atoyac–Puerto del Gallo, cañada al E de la carretera, *Contreras 1471* (FCME). Mpio. Cualác, 3.87 km al E de Cualác, *Cruz 7996* (FCME). Mpio.

Eduardo Neri, 2 km al NO de Amatitlán, *Soto 1203* (FCME). Mpio. General Heliodoro Castillo, Barrio Nuevo, 0.94 km al NE, *Soto 15311* (FCME); Tlacotepec, 9 km después de Yerba Santa carretera Filo de Caballo–Puerto del Gallo, *Contreras 1153* (FCME); Tlacotepec, 6.76 km al NE, *Cruz & Castrejón 4939* (FCME). Mpio. Ixcateopan de Cuauhtémoc, 3 km antes de Ixcateopan, al E, *Valencia 127* (FCME). Mpio. Leonardo Bravo, La Escalera, 5.97 km al E, *Soto 10840* (FCME). Mpio. Taxco de Alarcón, Tenoxcotitlán, 3 km camino a Noxtepec, *Cruz 1354* (FCME). Mpio. Teloloapan, Puerto del Aire, *Moreno & Serralde 90* (FCME). Mpio. Tlapa de Comonfort, 12 km al S de Olinalá, camino a Tlapa, *Martínez 1165* (MEXU). Mpio. Zirándaro de los Chávez, Zirándaro, a 1 km al E de Guayameo, camino a Placeres del Oro, *Soto 4937* (FCME, MEXU). **Oaxaca.** Mpio. Asunción Ixtaltepec, subida al Cerro Punta, al S de Mazahua, 13 km al NE de La Ventosa, *Torres 12600* (MEXU). Mpio. San Carlos Yautepec, La Hamaca, 580 m al E, sobre Río Zimatán, sobre brecha a Santa Catarina Jamixtepec, *Velázquez 392* (MEXU). Mpio. San Miguel Chimalapa, La Coralilla, Valle del Río Escondido, *Maya 574* (MEXU, CHAPA). Mpio. San Miguel del Puerto, 0.3 km de la desviación camino a Santa Catarina Jamixtepec, orilla de Río Zimatán, *Pascal 4* (MEXU). Mpio. Santa María Huatulco, Laguna de Chahue, *Castillo 9615* (MEXU, XAL).

Crotalaria cajanifolia, Cruz & Castrejón 4939, FCME.

Crotalaria lidiae, *Velázquez 637,* FCME.

Figura 2. Parte apical de las inflorescencias de *Crotalaria cajanifolia* y *C. lidiae.*

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OENANTHE JAVANICA (APIACEAE) NEW TO THE FLORA OF OHIO

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ABSTRACT

Oenanthe javanica, an invasive Asian species of Apiaceae, is reported here as a new addition to the flora of Ohio. The species has previously been reported in the USA from the District of Columbia, Georgia, Illinois, Maryland, Minnesota, Missouri, Virginia, and Wisconsin. Invasive potential of the species is great, especially in wet habitats.

The genus *Oenanthe* (Apiaceae) has been represented in Ohio by one species: *Oenanthe aquatica* (L.) Poir. (water-fennel, Cooperrider et al. 2001; vouchers *Cusick 25523*–MU, OS, and *Louden 4298*–OS), which is native to Eurasia and northern Africa (Cooperrider 1995). In 2017, a plant was found growing in a wet, shady depression along the hike/bike trail of the Little Miami Scenic River Trail in the Little Miami State Park, site of a former rail line. A voucher specimen was collected in 2018 and has been identified as *Oenanthe javanica* (Blume) DC., Java water dropwort (also known as Vietnamese parsley or water celery (SEWISC 2016)).

Voucher. **Ohio**. Clermont Co.: Little Miami State Park, N 39.2517º, W -84.2832º, 2 May 2018 *Becus 90218* (MU, NY).

The Ohio population consists of one long colony (approx. 6 meters by 1 meter) between the paved trail and the wooded hillside. The species has not been observed anywhere else along the trails in the park. The white flowers are produced mid- to late summer and fall, followed by the nearly globose fruits.

Key to species of *Oenanthe* in Ohio

1. Plants perennial; leaflets coarsely toothed, sometimes slightly lobed, leaves pinnate or bipinnate; peduncles 5–16 cm, longer than rays; fruits ca. 2.5 mm long, not demonstrably curved, styles nearly as long as fruits ..... **Oenanthe javanica**
1. Plants annual or biennial; leaflets finely subdivided into narrow, nearly liner, segments, leaves thus 3-4-pinnate; peduncles 1–3 cm, often shorter than rays; fruits 3–4.5 mm long, often curved, styles shorter than fruits ..... **Oenanthe aquatica**

Oenanthe javanica is native to Asia (Fading & Watson 2005) and cultivated as an edible species (Facciola 1990; Uphof 1968), even though other members of the genus are very toxic (Ball et al. 1987). The species is sometimes grown as an ornamental for aquascaping, especially the pink variegated cultivar 'Flamingo' (Missouri Botanical Garden 2020).

Oenanthe javanica has been previously reported in the USA from the District of Columbia (Simmons et al. 2008), Georgia (Kartesz 2015), Illinois (Illinois Wildflowers 2020), Maryland (Simmons et al. 2008), Minnesota (EddMapS 2020), Missouri (Yatskievych 2006; Yatskievych & Raveill 2001), Virginia (Simmons et al. 2008; Weakley et al. 2012), and Wisconsin (Flora of

Wisconsin 2020). It has strong potential as an invasive species in moist to wet habitats and has been banned in Wisconsin (SEWISC 2016).

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ADDITIONS TO THE NEW FLORA OF VERMONT—II.

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ABSTRACT

Twenty-seven species and one variety are newly reported for the flora of Vermont. Four species that have been reported elsewhere also are briefly summarized.

This is the second list of vascular plants not recorded in the New Flora of Vermont (Gilman 2015) but now vouchered from the state. The first list of additions (Gilman 2016) added 25 new taxa (22 species and 3 varieties) and recapitulated three other species that were reported elsewhere. Several other taxa remain under review for possible inclusion as members of the vascular flora of Vermont, including in the genera *Callitriche, Cyperus, Elatine, Mentha*, *Taraxacum*, and *Viola*.

The format of the entries is similar to that of the New Flora and the first list of additions.

ALISMATACEAE

1. *Sagittaria australis* (J.G. Sm.) Small, Fl. S.E. U.S. 45–46. 1903. Appalachian arrowhead.

Chittenden Co: Winooski, large island immediately downstream of Winooski Falls in drawn down wet gravelly sandbar flats east (upstream) of the upland part of the island; this area exposed, but usually under 1 ft of water, rare scattered plants, 17 Oct 2016, *Marcus s.n.* (VT).

The range extension of *Sagittaria australis* to a site on the Winooski River slightly upriver of where it enters Lake Champlain is noteworthy. The closest known locations are in New Jersey and Pennsylvania (Haynes & Hellquist 2000), more than 200 miles distant; reports from New York (e.g. Gleason & Cronquist 1991; Haynes & Hellquist 2000) are apparently in error (Werier 2017). The identification of the cited specimen was confirmed by R. Haynes (pers. comm. to A. Marcus, 17 Oct 2017). *Sagittaria australis* differs from the very common *S. latifolia* L. by its free, stiff, slightly fleshy vs. partially connate, lax, and chartaceous bracts and by achene beaks erect at base and slightly to strongly recurved above vs. horizontal. It is readily distinguished from the recently reported *S.*

engelmanniana J.G. Sm., which is rare in Vermont but occurs not far distant, by the lack of facial glands on the achenes and by recurved vs. merely ascending beaks of the achene; and from emersed forms of *S. cuneata* Sheldon by longer achene beaks that are inserted at the upper angle of the achene rather than at summit.

The mode of introduction to this aquatic system is unknown but was perhaps via cultivation as a water plant. The population is small (ca. 20 plants) and is confined to an alluvial (fine gravel mixed with coarse sand) mid-river island where plants are sometimes exposed to strong flows and subject to rapid inundation and exposure. This island is below the fall line, at an elevation of approximately 99.0 ft to 100.5 ft and is within the flood elevation of Lake Champlain so the habitat, while riverine, is subject to lake influence at high water. Despite a high-energy environment, the population has persisted at least four years, 2016–2019.

AMARANTHACEAE

2. *Chenopodium berlandieri* Moq. var. ***macrocalycium*** (Aellen) Cronq., Man. Vasc. Pl. N.E. U.S. (ed. 2) 863. 1991. Beach pit-seeded goosefoot.

Chittenden Co: Burlington, Starr Farm Beach, few on upper strand, 17 Oct 2018, *Gilman 18096* (VT); Starr Farm Beach, sandy beach exposed by low water levels of Lake Champlain, 44.515954, -73.268952, 27 Oct 2018, *S. Fawcett 1020, Gilman, Davis & Miller* (VT). Colchester: RR embankment, 12 Oct 1912, *Flynn s.n.* (VT-061841, VT-061853); Delta Park, high sandy beach north of the mouth of the Winooski River, a very low water year, 5 Oct 2016, *Gilman 16111, Marcus, and members of the Vermont Scientific Advisory Group – Flora* (VT, NEBC). Winooski: Winooski River, floodplain on N bank S of downtown, 44.48972N, -73.1966W, 30 Oct 2018, *Fawcett 1026 & Marcus* (VT).

As treated by Clemants and Mosyakin (2003), var. *macrocalycium* is a non-weedy beach-habitat variety of the widespread *C. berlandieri* and in Vermont is likely a relict of the ancient Champlain Sea along with such taxa as *Lechea maritima*, *Hudsonia tomentosa*, and *Lathyrus japonicus* var. *maritimus*.

It was excluded by Jenkins and Zika (1995), who noted that a Flynn specimen (VT-061853) annotated (at species rank) as *C. macrocalycium* by Wahl was a duplicate of one he annotated as *C. bushianum* Aellen (VT-061841) on the same date. Gilman (2015) concurred with this decision and also excluded this taxon from Vermont. Following Marcus's (2016) discovery of *C. berlandieri* on sand beaches of Lake Champlain in the Burlington–Colchester area, the Flynn specimens were reviewed and both were determined as var. *macrocalycium*. The recent collections are much-branched proximally with erect branches and relatively poorly toothed leaves, differing in aspect from var. *bushianum*, which has loosely arching-erect branches and more prominently toothed leaves. The Winooski River population, which occurs on a steep sandy riverbank and exposed damp sands at the base of the bank, consists of plants that are more robust than typically described (e.g., Haines 2011) from coastal habitats, sometimes growing to 1 m or more, perhaps a consequence of high available nutrient levels. Variety *bushianum* is also rare in Vermont, and we note that there has been little recent attention paid, locally and in general, to the systematics of these closely related but rather poorly defined varieties.

3. *Chenopodium ficifolium* Sm., Fl. Brit. 1: 276–277. 1800. Fig-leaved goosefoot.

Washington Co: Montpelier, US Rte 2, large plants on spoil pile (loam, gravel, sand) under I-89 overpass, 21 Aug 2010, *Gilman 10116* (VT-061094).

Based on its reticulate-honeycombed pericarp, this collection was cited in the New Flora of Vermont (Gilman 2015) as *C. berlandieri* var. *bushianum* (Aellen) Cronq., which was the only pit-seeded goosefoot known in Vermont at the time. Recent reviews of all available Vermont pit-seeded goosefoot material and additional fieldwork have resulted in revision of this collection. It conforms in pericarp ornamentation, seed-size (ca. 1.2 mm), and leaf shape with published descriptions and images of *C. ficifolium*; and conforms to the typical subspecies with basal leaf lobes that are antrorsely directed, vs. perpendicular to the leaf axis in ssp. *blomianum* (Aellen) Aellen (Mosyakin 2016). In North America, this species is considered introduced or adventive from Europe and Asia (Clemants and Mosyakin 2003).

4. *Dysphania pumilio* (R. Br.) Mosyakin & Clemants, Ukrayins'k Bot. Zhurn., n.s. 59(4): 382. 2002. Clammy glandular-goosefoot.

Rutland Co: Rutland, Post Road, just NE of Vermont National Reserve facility, abundant weed in small field of corn, soybeans, and pumpkins, 13 Sep 2018, *Gilman 18073* (VT, NEBC).

This is an annual agricultural or ruderal weed (e.g., common in New York City, D. Werier, pers. comm.), originally from Australia but now more or less cosmopolitan (Clemants & Mosyakin 2003). Zhang and Zhu (2016, 2017) transferred it and two other non-native Vermont weeds, *D. botrys* L. and *D. ambrosioides* L. from the genus *Dysphania* to the resurrected genus *Neobotrydium* Moldenke, based on their dichasial-cymose (vs. spicate or paniculate) inflorescences. These species all share strongly aromatic, yellowish, globose glandular hairs.

APIACEAE

5. *Myrrhis odorata* (L.) Scop., Fl. Carniol. ed. 2, 1: 207. 1771. Sweet Cicely.

Orleans Co: Craftsbury, W side of Vt. Rte. 14, a short distance N of Eligo Pond, 11 Jun 2016, *Gilman 16024* (VT-288703, NEBC).

Sweet Cicely, a native of Europe, differs from other local Apiaceae in rather densely pubescent, finely divided leaves that are often mottled with small whitish patches, and elongate, anise-scented fruits. It is somewhat reminiscent of the very invasive *Anthriscus sylvestris* (L.) Hoffm., but the upper leaf-sheaths are not inflated, the inflorescences are broader and more erect, and the fruits are strongly ridged (Tutin 1980). It is frequently grown by herbalists and landscapers for its anise-scented seeds, attractive foliage, and large umbels of white flowers, and it is sometimes observed spreading near gardens (Gilman, personal observation). The Craftsbury collection, however, was from a large roadside patch not associated with any residence. It is also known as a local escape in Massachusetts and Connecticut (CNH 2019).

6. *Selinum carvifolia* (L.) L., Sp. Pl., ed. 2, 350. 1762. Little-leaved angelica.

Bennington Co: Mt. Tabor, large patch, ditch and edge of damp pasture, US Rte. 7, 4 Sept 2004, *Gilman 04179* (VT-085810, VT-085830). Sunderland: A number of tall plants along logging road, just upslope, E side of Batten Kill, near River Road just S of Manchester town line, 14 Nov 2001, *Gilman 01184* (VT 085809).

Following collection of the above-cited specimens from disturbed, rather open habitats, the senior author long assigned them to *Conioselinum chinense* (L.) Britton, Sterns, & Poggenb., which, however, is a species that occurs in undisturbed, forested wetlands, riverbanks, and seepy ledges. Upon recent re-examination, they were shown to be *Selinum carvifolia*, a native of Europe and western Siberia (Pimenov 2018). Although it shares the character of 3-winged mericarps, *Selinum* differs from *Conioselinum* in having pubescent/scabrous rays (Tutin et al. 1968) and narrower, more tightly clasping

upper leaf sheaths (Reduron 2018). Despite their close resemblance, Downie et al, (2010) found the two not to be closely related. The different clades to which they belong are in a large polytomy in the crown group of Apiaceae subfamily Apioideae (Downie et al. 2010).

Selinum carvifolia has only twice been reported for North America. The first report was of a 1908 collection that was stated (Knowlton & Deane 1922) to have been made at a vacant lot in Boston, MA; however, a specimen supporting that record has not been seen, and a recent search on various portals of herbarium databases (CNH, SERNEC, SEINet) has failed to locate such a specimen. The second report is current, from Tompkins Co., New York (Werier 2017), where the population is said to be "maintaining itself." It is a perennial herb (Tutin 1980) but its persistence in Vermont since 2014 is not known.

7. *Torilis japonica* (Houtt.) DC., Prodr. 4: 219. 1830. Japanese or erect hedge-parsley.

Bennington Co: Pownal, North Pownal, seasonally saturated floor of former quarry, 17 Jul 2018, *Standley s.n.* (NEBC-01621348); North Pownal, Quarry Hill, along trail to quarry at bottom of hill, 17 Jul 2018, *Grunden* (MAINE); Adjacent to Rte. 346, 42.792149 -73.255396, WGS84, 75-100 individuals, occasional along paths and in understory below old limestone quarry (Nature Conservancy property), 31 Jul 2018, *Doucette 07311801* (VT); Adjacent to Rte. 346, 42.792390, -73.255005, WGS84, 75-100 individuals, occasional along paths and in understory below old limestone quarry (Nature Conservancy property), 31 Jul 2018, *Doucette 07311802* (VT); Adjacent to Rte. 346, 42.792360, -73.254073, WGS84, 75-100 individuals, occasional along paths and in understory below old limestone quarry (Nature Conservancy property), 31 Jul 2018, *Doucette 07311803* (VT); Adjacent to Rte. 346, 42.792348, -73.255891, WGS84, 75-100 individuals, occasional along paths and in understory below old limestone quarry (Nature Conservancy property), 31 Jul 2018, *Doucette 07311804* (VT). **Windsor Co:** Hartland, disturbed forest edge along Eastman Road above US Rte. 5, small colony of 5 fruiting plants and dozens of vegetative rosettes, 30 Sep 2019, *Peters s.n.* (VT).

This species was first introduced into North America in 1917 and, following a lag of nearly a century, has recently raised concern as an invasive species (DiTomasso et al. 2014), at least in the northeastern and north central United States, and southern Canada. It is similar in ecology to another non-native member of Apiaceae, *Anthriscus sylvestris* (L.) Hoffm., that has spread rapidly throughout much of Vermont as a roadside weed and adjacent fields and forest margins. It is, however, readily distinguished morphologically from that species by its solid stems, spinulose mericarps, and later, midsummer, bloom. In England, where both are native, *Torilis japonica* is said to be the most common, summer-flowering roadside umbellifer, and *Anthriscus sylvestris* the most common early-flowering one (Tutin 1980).

ARACEAE

8. *Wolffia brasiliensis* Wedd., Ann. Sci. Nat., Bot., sér. 3, 12(3): 170, t. 8 f. 1–23. 1849. Brazilian water-meal.

Windham Co: Vernon, Connecticut River shore, extensive mixed colonies with *W. borealis* in shallow water with abundant floating wrack and debris at portage trail just above Vernon Dam, 31 Oct 2016, *Peters s.n.* (VT).

Wolffia brasiliensis, originally described from Brazil, was long known in North America under its synonym *W. punctata* Grisebach (Landolt 1986). It occurs more or less throughout the eastern portion of the United States and has been known from the Connecticut River in neighboring Massachusetts since the 1970's (CNH 2019).

As a genus, *Wolffia* has been slowly colonizing western Vermont for nearly a century. *Wolffia columbiana* was first documented in southern Lake Champlain in 1929 (*Muenscher, Manning and Maguire No. 306*, VT-050629, VT-050631) and has now spread throughout that system and other waterbodies in western Vermont. It is now considered invasive in Europe, where it appears to be impacting indigenous *W. arrhiza* (L.) Horkel (Schmitz et al. 2014; Verloove 2019). *Wolffia borealis* (Engel.) Landolt & Wildi has been known since ca. 1980 (including the Zika specimens discussed below) and it, too, is present more or less throughout the Champlain Valley. Given this pattern, the discovery of a third watermeal, *W. brasiliensis*, in the Connecticut River, not far north of known populations in the same river system in Massachusetts was to be expected. Its presence is likely due to a natural range expansion, perhaps with waterfowl as vectors.

This taxon was not treated in the New Flora of Vermont (Gilman 2015) as a member of the flora or as an exclusion, and this lapse is here corrected. It had been mapped by Angelo and Boufford (2000) for Vermont: Bennington County and, in turn, this report was the basis for Vermont's inclusion on the Biota of North America (BONAP) county-distribution map of the species (Kartesz 2014). The underlying basis of the report was a collection made in 1980 by Peter Zika, labeled as *W. punctata* (a synonym of *W. brasiliensis*) from Bennington Co: Manchester, *Zika 2276* (VT-050637, MASS-00339969, MASS-00339970). The specimen of *Zika 2276* at VT was reexamined—the fronds re-wetted and viewed under a 20× dissecting scope—and determined to be *W. borealis*, with fronds clearly plane across the upper surface. *Wolffia borealis* was also long known, mistakenly, as *W. punctata* (Landolt 1986), the likely source of the error.

ARALIACEAE

9. Eleutherococcus sieboldianus (Makino) Koidz., Acta Phytotax. Geobot. 8(1): 52. 1939.
Five-leaved aralia.

Windham Co: Dummerston, [518] Kipling Road, May 2018, *Guenther s.n.* (VT).

Introduced from Japan for ornament, this is now sparingly escaped in southern New England (Haines 2011; Cullina et al. 2011) and, in particular, there are several specimens in regional herbaria from the Connecticut River valley in Massachusetts (CNH 2019). It is shrubby, with palmately 5-divided leaves and is overall somewhat reminiscent of the popular 7–9 leaflet houseplant, *Schefflera arboricola* (Hayata) Kanehira, differing by being cold-hardy and by having somewhat thorny stems. Another species, *E. senticosus* (Rupr.) Maxim, is named "Siberian ginseng," implying a relation of this genus to ginseng, *Panax* L. but, although close, the two are not in sister clades (Kim et al. 2017).

ASTERACEAE

10. *Inula racemosa* Hook. f., Fl. Brit. India 3(8): 292. 1881. Himalayan elecampane.

Caledonia Co: Hardwick, Hardwick Farms Road, escaped from cultivation to margins of corn (maize) fields and ditches, Hardwick Farms property. Stated by landowner to have been planted from seed acquired from the Royal Horticultural Society (Wisley) ca. 25 years previous but spreading (by seed) over distances 150m to farmland and said to be grazed by (Jersey) cows, 30 Sep 2017, *Gilman 17137 & J. Laggis* (VT-289445, NEBC). **Washington Co:** Marshfield, Hollister Hill Road, near parking area for Stranahan Town Forest, but well removed from and across the road from a possible garden source, small group, several plants, rough ground, thick pasture, 12 Oct 2019, *Gilman 19060* (VT).

Himalayan elecampane is here reported as new to North America. *Inula racemosa* is a striking plant: tall (to 2m), with large, felted leaves, and a strictly erect, many-flowered racemiform capitulescence (occasionally with short, ascending, few-flowered branches) of large (5 cm) yellow-rayed capitula. The foliage and flowers are nearly identical to those of common elecampane (*Inula*

helenium L.), also non-native, which is moderately common in damp pastures and fields throughout Vermont, but that species has a few-flowered, broadly paniculiform capitulescence.

The collections cited are obvious escapes from ornamental horticulture, the first from a known seed source and the second from a nearby, but hardly adjacent, garden. This second population was first brought to the senior author's attention via a posting on *i*Naturalist by local resident Erika Mitchell (*i*Naturalist 2019).

The species is originally from the western Himalayas at altitudes of 1525m–2750m (Hooker 1881), but its introduction to North America is via Europe (England). Based on observation of these local populations, its ease of dispersal by windblown achenes with long pappi, and the widespread presence of the similar *Inula helenium* in New England, it seems likely that this is potentially an invasive species. It has also been reported as an overlooked, potentially invasive plant in Belgium (Verloove 2008).

11. ***Liatris pycnostachya*** Michx, Fl. Bor.-Amer. 2: 91. 1803. Prairie blazing-star.

Caledonia Co: Burke, pipeline corridor at summit, toward Victory, only one plant, 3 Sep 2017, *Gilman 17087* (VT). **Windsor Co:** Rochester, NAD83 N 44.868414/E-72.880787 +/-30m, north shoulder of Camp Brook Rd just south of wet road ditch and wet meadow on dryer shoulder, in open field at Riley Bostwick WMA, east of the brook crossing at the big dip in the road, just one roadside plant in flower, likely arrived by seed from a garden in the area—probably via a vehicle or wind, 19 Aug 2019, *Marcus s.n.* (VT).

This is an easily grown garden perennial and relatively popular in horticulture. Generally a species of the midwest and middle south, it is also known as a garden escape from other eastern states (Nesom 2006; Haines 2011). Its pappose achenes are readily wind-dispersed. The specimens reported here were of single individuals, confirming their status as waifs; another such plant observed in Essex County persisted three years and then vanished (Gilman, pers. obs.). We feel reporting of such waifs is justified, even if the plants are transient and no populations are formed, for sake of completeness and alignment with herbarium databases (see *Kummerowia*, below, also a waif). It is possible that, in the future, populations may become established and, if so, these first reports will be useful.

12. ***Petasites japonicus*** (Sieb. & Zucch.) Maxim., Award 34th Demidov. Prize 212 1866. Japanese sweet-colt's-foot.

Chittenden Co: Burlington, forested seasonal drainage way, wet area SW of 71 Little Eagle Bay, 29 Apr 2016, *Kruesi* (VT).

Originally from East Asia, and introduced to Vermont (likely via Europe, as many horticultural plants have been) this species has been occasionally grown, especially since the 1990's (K. Kruesi, pers. comm. to Marcus) for ornament or interest due to its very large, boldly architectural foliage. In gardens, it can spread aggressively, and it appears to be incipiently invasive (VT Invasives 2019). Various unvouchered reports have been made on websites, e. g. from Windsor Co: Woodstock (The Vermont Journal 2019). There were, as of 30 December 2019, nine Vermont observations of this species posted in the citizen-scientist website *i*Naturalist (2019) although it is unclear if some are from garden settings. Habitats generally appear to be in wet soil in seeps and along ditches, streams and rivers. Spread appears (to date) to be primarily vegetative—anecdotally, it is considered by those with experience in cultivating it to be a very aggressive, "impossible to control" spreader. As noted by Gilman (2016), collection of vouchers of invasive species often lags well behind the actual invasion.

13. ***Verbesina alternifolia*** (L.) Britton ex Kearney, Bull. Torrey Bot. Club 20(12): 485. 1893. Wingstem.

Windsor Co: Bethel, large patches along road and spreading widely into horse pasture, River Road (Finlay Bridge Road), not far S of Randolph town line, 5 Sep 2016, *Gilman 16102* (VT-289447, NEBC).

Wingstem occurs throughout the Midwest and the interior eastern United States as far north as New York (Kartesz 2014), where it is of unknown nativity (Werier 2017). In New England it is known only from Massachusetts, where it is not considered indigenous (Cullina et al. 2011; Haines 2011). Here, this population seems to have been introduced horticulturally but has spread into a neighboring field and also some distance along the local, unpaved road. Wingstem has not been suggested to have invasive potential.

14. ***Vernonia noveboracensis*** (L.) Michx., Fl. Bor.-Amer. 2: 95. 1803. New York ironweed.

Chittenden Co: Shelburne, ca. 10 clumps, stout, on semi-managed utility corridor (buried electric and sewer), suburban area, E side RR tracks, between tracks and forest patch, just S of Clearwater Road, 6 Sep 2018, *Gilman 18066* (VT, NEBC).

New York ironweed is indigenous in neighboring New York and Massachusetts. It is locally somewhat popular in horticulture, so it is unsurprising that it should be a casual escape. At the cited location, it was out of sight of houses and the population was scattered. Plants were typically robust, to 2m tall.

CARYOPHYLLACEAE

15. ***Paronychia fastigiata*** (Raf.) Fern. var. ***fastigiata***, Rhodora 38: 421. 1936. Hairy forked whitlow-wort.

Windham Co: Wilmington, gravel parking lots and road margins around the maintenance shop at the Hermitage ski resort, 18 Sep 2016, *Peters s.n.* (VT-288392).

This species, native to North America, is apparently only adventive to Vermont, the current population perhaps brought in by earth-moving equipment or in the gravel itself. An earlier report (Angelo & Boufford 2012) from Addison County, was likely based on a specimen collected in 2001 in Addison Co: Middlebury (*A. Turner A701-104 & W. Brumback*, VT-063137). That collection was noted in the New Flora (Gilman 2015) as missing but is now in the proper folder at VT. It was re-examined for this effort and determined to be a non-flowering specimen of *Moehringia lateriflora* (L.) Fenzl, so the report is herein excluded. The current collection is of the typical variety, characterized by straight styles and short (<0.15 mm) tips ("cusps") of the sepals.

CYPERACEAE

16. ***Cyperus erythrorhizos*** Muhl., Descr. Gram. 20. 1817. Redroot flatsedge.

Addison Co: Cornwall, Lemon Fair River, large and vigorous fruiting plants up to 0.5m tall on silty clay river shore, 9 Oct 2014, *Engstrom s.n.* (VT). **Chittenden Co:** Burlington, Elks Club Beach near Lone Rock Point, lake sand beach, upper and mid-level strand lines of annual plant growth in low lake level summers, 5 Sep 2018, *Kruesi 202* (VT-290708). Charlotte, Converse Bay, drawn down sand beach, Oct 2016, *Marshall s.n*. (VT). Colchester, Delta Park, shore of Lake Champlain, 5 Oct 2016, *Marcus s.n.* (VT); same, 5 Oct 2016, *Gilman 16113 & Flora Advisory Group* (VT-289467). Shelburne, Shelburne Town Beach, wet sand, full sun, 44°21'43"N, 73°15'60"W, 29 Sep 2016, *Sopher 70* (VT-289238). South Burlington, Queen City Park, shore of Lake Champlain, 8 Oct 2019, *Peters s.n.* (VT). Winooski, Winooski River, north shore, Salmon Hole, on drawn down sands, 25 Sep 2017, *Marcus s.n.*

(VT). **Grand Isle Co:** South Hero, dunes, 18 Oct 2016, *Popp 2606* (VT). **Windham Co:** Vernon, Connecticut River shore, on sand/gravel bars in drawdown zone just above and below Vernon Dam, 18 Oct 2016, *Peters s.n.* (VT). **Windsor Co.:** Bethel, [2nd Branch White River], just N of Findlay Bridge, occasional on exposed gravel bar, 5 Sep 2017, *Gilman 16098* (VT-289466).

This common flatsedge of eastern North America was first reported, with photos, as an unidentified *Cyperus* on the citizen-scientist website, iNaturalist.org, from two sites in Addison County, first by Charlie Hohn (iNaturalist 2012) and second by Susan Elliott (iNaturalist 2013). However, the species was not identified or vouchered in Vermont until a third site was discovered by Engstrom in Addison County in 2014. It was collected shortly thereafter in Chittenden, Grand Isle, Windham, and Windsor Counties. It was previously known in the surrounding states (Tucker 2002) and was first found in neighboring Quebec in 2007 (*Sabourin & Lavoie 2817*, MT-00023146).

In October 2016, the water level on Lake Champlain (93.75 ft.; https//nwis/waterdata.usgs.gov) was well below its ordinary low level (94.46 ft., Morgan 2014) and nearly two feet below its mean elevation (95.63 ft., Murphy 2014). A field trip was organized by Vermont's Scientific Advisory Group – Flora (which is advisory to Vermont's Endangered Species Committee) to the exposed beaches at Delta Park, on the shore of Lake Champlain at the mouth of the Winooski River, Colchester, for the purpose of observing rare littoral species such as *Eleocharis diandra* C. Wright, *Sparganium androcladum* Morong and *Cyperus diandrus* Torr. On that trip, *Cyperus erythrorhizos* was observed to be abundant on saturated but exposed gravelly sand and sandy silt beaches. That it was found at many widely distant sites within a short period of time—and is quite conspicuous—is (at least in part) an example of "plant blindness" (Wandersee and Schussler 2001).

FABACEAE

17. *Kummerowia striata* (Thunb.) Schindl., Repert. Spec. Nov. Regni Veg. 10(257/259): 403: 1912. Japanese-clover.

Windham Co: Vernon, Connecticut River shore, one single plant growing on exposed shore/beach at public water access just below the Vernon Dam, 18 Oct 2016, *M. Peters s.n.* (VT-228936).

Japanese-clover was introduced into North America from Asia, and has been extensively cultivated, especially in the southeastern United States where it is "ubiquitously established" (Isely 1998) and where it has caused some concern as an invasive species (Gucker 2010). Its mode of introduction to Vermont is unknown.

The genus *Kummerovia* Schindl. has recently been considered sister to *Lespedeza* Michx. (Xu et al. 2012), with which it shares a one-seeded loment and leaves with 3 leaflets, but from which it differs in prominent, striate stipules, annual habit, and flowers inserted singly. However, it was earlier treated in North American literature (e.g. Fernald 1950) as *Lespedeza striata* (Thunb.) Hook. & Arnott, and botanists have struggled to find its relationships; the taxonomic history of its tribe, Desmodieae (Benth.) Hutchinson, is complex. This history was summarized by Ohashi and Nemoto (2014), who also recognized it as sister to *Lespedeza*. A recent molecular study (Jabbour et al. 2018), however, suggests that the genus is nested within *Lespedeza*, in which case the name of our species would be *Lespedeza striata* (Thunb.) Hook. & Arnott.

GERANIACEAE

18. *Geranium sibiricum* L., Sp. Pl. 2: 263. 1753. Siberian crane's-bill.

Franklin Co: Highgate, hedgerow at edge of sandy lawn, does not appear cultivated, Lamoille Valley Rail Trail, E of Vt. Rte. 105, just E of village, 5 Oct 2018, *Gilman 18065* (VT, NEBC).

Eurasian in origin, Siberian crane's-bill has been known in North America at least since the late 19th century, either as a naturalized plant (Watson & Coulter 1890) or as an adventive (Britton and Brown 1897). It is known from several northeastern states (Aedo 2012; Kartesz 2014) and has recently been found in Québec (Blondeau 2015). The current population, although near a lawn, was in a rail-trail corridor and did not appear to have been cultivated; it formed a large patch. Individual stems in this collection are slightly atypical with 2 flowers, not one, on each pedicel, a character stated (Xu and Aedo 2008, Aedo 2012) to occur on occasion.

LAMIACEAE

19. *Lycopus europaeus* L., Sp. Pl. 1: 21. 1753. European water horehound.

Chittenden Co: Burlington, Starr Farm beach, wet area (rill) at top of beach, 18 Oct 2018, *Gilman 18097* (VT). Shelburne, occasional on shoreline of the LaPlatte River at Shelburne Falls, 4 Sep 2018, *Gilman 18057* (VT); bank of the LaPlatte River, W of the RR tracks W of US Rte. 7, 5 Sep 2018, *Gilman 18058* (VT).

European water-horehound has invaded shores and waterways in eastern North America since the 1860's, with a rather rapid invasion along the St. Lawrence River downriver of Lake Ontario since the 1960's (Stuckey & Phillips 1970). A horse-collar shaped ring of corky tissue around the crest of the nutlet is a flotation device that adapts the species to rapid water-borne dispersal (Moon and Hong 2006). Delisle et al. (2003) indicated that, in Québec, the spread was "almost exclusively along the course of the St. Lawrence River" and estimated a colonization rate of ca. 45 km/year. Given that there is often a significant lag time between colonization and discovery of a colonizing species, it is likely that this species now occurs, or will soon occur, throughout Lake Champlain and its environs.

20. *Mentha aquatica* L. var. ***citrata*** (Ehrh.) W.C. Werner, Bull. Techn. Serv. Ohio Agric. Exp. Sta. 1(3): 239. 1893. Water mint, orange mint, bergamot mint.

Washington Co: Calais, Worcester Road, Curtis Pond fishing access area, 12 Aug 2017 [flowers] & 18 Oct 2017 [fruit], *Gilman 17067* (VT, NEBC).

A previous report of *Mentha citrata* (Atwood et al. 1973) from Bennington County was based on two non-flowering specimens from North Dorset, collected by N.F. Flynn on 27 May 1900 (VT-126881) and on 27 Aug 1900 (VT-126882). The first is apparently a seedling and the second is a stoloniferous shoot. These specimens cannot be confidently identified. A second report by Atwood et al. (1973), from Windsor County, was based on a specimen from Bethel collected as *M. spicata* L. by P. Spalding without recognizable date (NEBC-00573346), and later annotated by F.C. Seymour as *M. citrata* Ehrh.; this specimen was still later annotated by H. Ahles as *M. piperita* and is currently filed as such. No specimen has been seen to support a third report by Atwood et al. (1973) from Franklin County. A fourth report, from Lamoille County, underpinned by another specimen at VT, collected at the Trapp Family Lodge in Stowe by M.R. Carse on 16 Sep 1971 (VT-126880) was possibly from cultivation from the well-known and rather extensive gardens at that resort.

The Calais population is extensive and robust, occurring in a damp but not marshy area near Curtis Pond. Plants have a distinctive strong scent that is faintly citrusy and faintly spicy, as implied by both its common and scientific names. The exact taxonomic placement of this plant is uncertain. Originally described as a species, it has been widely treated as a variety of *M. aquatica* but according to Harley (2015) it may have arisen as a hybrid between an unusual fertile form *M. aquatica* and *M. spicata* (spearmint), resulting in a sterile *M.* ×*piperita* L. var. *citrata* (Ehrh.) Briq. Like other sterile mints on the Vermont landscape, it is likely an introduction from Great Britain.

21. ***Mentha longifolia*** (L.) L., Amoen. Acad. Linnaeus ed. 4: 485. 1759. Horse mint.

Washington Co: Barre, Lower Usle Road, ditch between two abandoned farm fields (becoming residential area), 11 Aug 2017, *Gilman 17066* (VT).

Mentha longifolia is easily mistaken for pubescent forms of spearmint, *M. spicata* L. (Tucker & Fairbrothers 2000; Tucker 2014), of which it is a progenitor, but identification of the current collection as *M. longifolia* is confirmed by its sessile, lanceolate-oblong, non-rugose leaves with sharp, spreading-arching teeth, by its abundant silvery, unbranched pubescence, and by its short anthers (Šarić-Kundalić et al. 2009). Specimens are a good match for the lectotype specimen chosen and illustrated by Tucker et al. (1980) and key out to *M. longifolia* in the keys provided by Harley (1972), Haines (2011) and Tucker (2014). Furthermore, although Tucker et al. (2005) found that *M. longifolia* may rarely have the characteristic aroma of *M. spicata*, the current population lacks it and is musty-scented with a hint of peppermint, as described by Tucker (2014) for *M. longifolia*. It is also noteworthy that pubescence has been selected against in the cultivated history of spearmint (Voss 1996; Harley 2016) and pubescent forms of spearmint are very rare in Vermont (Gilman, pers. obs.).

This species was likely introduced for cultivation from Europe; only one large clump, was observed. It is a fertile, diploid species, and may be anticipated to spread by seed.

ONAGRACEAE

22. ***Oenothera clelandii*** Dietrich, Raven, & Wagner, Ann. Missouri Bot. Gard. 70(1): 196. 1983. Cleland's evening primrose.

Chittenden Co: Milton, > 200 individuals, in two separate subpopulations; dry sand in sunny, open borrow area between US Rte. 7 and I-89 at near Checkerberry Corner, 5 Oct 2018, *Gilman 18093 & Briggs* (VT, NEBC).

Native to the Midwest, Dietrich and Wagner (1988) considered that populations from eastern states east of Michigan "may represent introductions" and it was treated as non-native in New York ("plants that occur or occurred … only as the result of human assistance") by Werier (2017). This seems the best interpretation for Vermont as well, given the habitat of the current population in a sandy, relatively recent borrow area. Sandy soils are extensive in the Milton area and several regionally common psammophilous species co-occur, including *Cyperus lupulinus* (Spreng.) Marcks, *Dichanthelium columbianum* (Scribn.) Freckmann, *Lechea intermedia* Legg. ex Britton, and *Trichostema dichotomum* L., but this species has not been previously observed elsewhere in the region.

PAPAVERACEAE

23. ***Hylomecon japonica*** (Thunb.) Prantl ex Engler & Prantl, Nat. Pflanzenfam. 3(2): 139. 1889. Forest-poppy.

Washington Co: Montpelier, W side of North St. heading out of town near where the bike trail starts, NAD83 N44.270394/E-72.561795+/300m down the road**.** One large clumped herbaceous patch on edge of street, and 1 large clump about 20ft west in woods. Plants are prominent in flower, and no more seen from the road. Probably a very new garden escape. Houses are nearby, but all on the other side of the road, so clearly now wild. 2 Jun 2017, *Marcus s.n.* (VT).

Forest poppy is native to China, Japan, Korea, and Russia (Siberia); see Zhang & Grey-Wilson (2008) for a technical description. It is an early-spring bloomer with single (4-petal) yellow flowers and is occasionally cultivated, especially by rock-gardeners and connoisseurs of difficult-to-obtain perennials (D. Avery, Cady's Falls Nursery, pers. comm to Gilman). This record documents a small but apparently persistent escape from horticulture; the specimen comports with the description of the

typical variety, with the basal leaf lobes biserrate rather than deeply incised of lobed. It is apparently new to North America as a wilding.

PHRYMACEAE

24. *Erythranthe guttata* (Fisch. ex DC.) Nesom, Phytoneuron 2012–39: 43. 2012. Yellow monkey-flower.

Washington Co: Middlesex, Wrightsville Dam State Recreation Area, Shady Rill town picnic area off Shady Rill Road, in a forested seep with *Juncus ensifolius*, with no recent signs of disturbance or horticulture, 660 ft elevation, 7 Jul 2018, *Marcus s.n.* (VT). **Windsor Co.:** Reading, no date [prior to 1915], [*P. W.*] *Whiting* (VT ex Hartland Nature Club).

A species of the American West, *Erythranthe guttata* is known in several locations in the northeastern USA (e.g., Haines 2011; Werier 2017). The Windsor County specimen was reported (as *Mimulus guttatus*) by Eggleston et al. (1915) and Dole (1937), but knowledge of this voucher was subsequently lost to later authors (Seymour 1969; Gilman 2015). It resurfaced when the herbarium of the Hartland Nature Club (located in Hartland, Windsor County) was donated to the University of Vermont, where it is now incorporated with the Pringle Herbarium. With this rediscovery, yellow monkey-flower is readmitted to the flora of Vermont.

Recently, a collection has been made from a substantial, well established population in Washington County, where a colony was established in a forest seep near a public picnic area. No mode of introduction is known for either collection but, over time, yellow monkey-flower has been grown for ornament in public and private gardens more or less worldwide, and seeds are widely available for purchase. The Washington County collection has been identified as the species in the strict sense (G. Nesom, pers. comm. to A. Marcus).

POLYGALACEAE

25. *Polygala vulgaris* L., Sp. Pl. 2: 702. 1753. Common milkwort.

Franklin Co: Fairfield, near Ridge Road, small group in mowed path through old field, mesic, 23 Jun 2019, *Dodge s.n.* (VT); 25 Jun 2019, *Gilman s.n. & Dodge* (NEBC).

Common milkwort (type of the genus *Polygala*) is a relatively common species in Europe, where it grows in grassy swards (McNeill 1968). It is said (McNeill 1968; Stace 2019) to be extremely variable as to flower color with white, pink, reddish, or blue flowers. The current population is growing among rather dense grasses in an old pasture or hayfield; flowers are a vivid, deep blue (Gilman, pers. obs.).

A relatively small, slender plant, common milkwort is a short-lived perennial and (at least in Europe) is dispersed by ants (Lack and Kay 1987). It is known as a sporadic introduction in North America from British Columbia (CPNH 2019), Michigan, (Voss 1985), WA (CPNH 2019), Oregon (CPNH, 2019) and California (SERNEC). Voss (1985) indicated that its presence was "undoubtedly an escape from cultivation" but it is not clear how the Vermont population was established. Its discoverer, Michael Dodge, is originally from England, but has long been a resident of Vermont. He operates a small nursery specializing in willows (*Salix* spp.), but the population is on a neighboring property.

POLYGONACEAE

26. *Rumex pseudonatronatus* (Borbás) Borbás ex Murbeck, Bot. Not. 1899: 16. 1899. Finnish dock.

Franklin Co: Swanton, Tabor Road, Missisquoi National Wildlife Refuge, tall plants in field, near parking, 26 Aug 2018 & 8 Sep 2018, *Gilman 18055* (VT, NY). Fairfax: Tall plants in dry, sandy

field, corner Vt. Rte. 104 and Sand Hill Road, 8 Sep 2018, *Gilman 18064* (VT, NEBC). **Chittenden Co.:** South Burlington: City of S. Burlington property S of Nowland Farm Road, common in field, 9 Oct 2018, *Gilman 18101* (VT, NEBC).

Finnish dock is a non-native European weed that is common in Canada in the Prairie Provinces (Mosyakin 2005). It appears to have spread into northwestern Vermont from adjacent Québec, where it was first documented a few years before being found in Vermont (Lavoie et al. 2012, CNH 2019). In Vermont it occurs as a scattered weed of old, seldom-mowed fields. Seed is abundantly produced and its biology is likely similar to that of other European docks that are common in the agricultural and roadside landscape in Vermont, e.g. *Rumex crispus* L., *R. longifolius* DC., and *R. obtusifolius* L., and it seems to be an increasing element of the landscape, at least in the northern Champlain Valley. It can be identified by its tall (1.5m), erect flowering/fruiting stem with relatively short, spreading to ascending, mostly distal branches, and relatively small, orbicular, entire outer tepals that lack tubercles. Plants are usually single-stemmed and do not form large clumps, and the branching pattern—the side branches are quite short and spreading—is quite distinctive.

RANUNCULACEAE
27. *Myosurus minimus* L., Sp. Pl. 1: 284. 1753. Tiny mousetail.

Windham Co: Dummerston, 500-1000 plants, NE corner of town in cornfield behind Soundview Paper Co. on way to Dummerston Landing, 13 May 2018, *Anderson s.n.* (VT).

Myosurus has a more or less circum-temperate distribution and is native in much of North America, especially in the western regions (Whittemore 1997). It is a rare weed in New England, known to date from a single collection from 1988 in Bristol County, Massachusetts (*Sorrie 4179*, GH-0643952), where it was stated to occur in a fallow field with "clayey, raw soil." Soils in the field noted on the collection label of the current record are mapped by USDA NRCS (2014) as silt loams, and the site may be subject to inundation by the nearby Connecticut River. Its ecology as a short-lived, early season annual, lends itself to weediness in certain conditions and in some areas it is a weed in agriculture, especially on damp soils (e.g., Fishel et al. 2000). Its presence in Vermont is likely a result of agriculture but its future under current management regimes is unknown.

SALICACEAE
28. *Salix serissima* (Bailey) Fern., Rhodora 6: 6–7. 1903. Autumn willow.

Addison Co: Cornwall, Cornwall Swamp, a few ~2m tall plants in small openings in the middle of the swamp, with mixed canopy of *Thuja occidentalis, Acer rubrum, Picea mariana* and scattered supercanopy of *Pinus strobus*, hummocky ground, 16 Jun 2016, *Engstrom s.n.* (VT). **Bennington Co.:** Pownal, White Oaks fen, W of White Oaks Road, rich fen with *Carex schweinitzii*, 29 May 2019, *Marcus s.n.* (VT).

Following long-standing but erroneous reports, as detailed below, autumn willow has been identified in two Vermont locations, both in calcareous fen/swamp habitats similar to those described for the species in western Massachusetts (Sorrie 1987). The first Addison County population was first discovered and photographed by Engstrom on 11 September 2014; his 16 June 2016 collection is from a male clone and includes remnant staminate aments.

Autumn willow has been reported or mapped from Vermont in several publications (Dole 1937; Seymour 1969; Atwood et al 1973; Argus 2007, 2010; USDA 2019) but historical reports have been in error. Most reports have been based on two collections. The first was made in 1920 by C.H. Knowlton from Bennington Co: Arlington (NEBC-00653895). Jenkins and Zika (1995) considered this specimen inadequate for determination but North American *Salix* specialist George Argus later (1997) annotated

it as *Salix lucida* Muhl.; an unannotated duplicate is at the Deam Herbarium, Indiana University (IND-0071490) (CNH 2019). The second collection, reported by Seymour 1969 and Atwood et al. 1973, was made by E. Anderson et al. in Orange Co.: Corinth in 1933. Jenkins and Zika (1995) were unable to locate that specimen, which at the time of their research was perhaps on loan to Argus. A sheet of that collection is now at NEBC (00653880) and it, too, has been annotated (1997) by Argus as *S. lucida*. Jenkins and Zika (1995) also determined mislabeled specimens from Franklin County (*no collector cited*, HNH) and Orleans County (*Churchill*, HNH) as *S. lucida*.

Despite the frequent misidentification of *Salix lucida* as *S. serissima*, and although they may often share the same habitat, the two species differ in numerous characters as detailed by Fernald (1904) and by Argus (2010). Additional characters of the buds, bud scales, and cataphylls are provided by Zinovjev (2010). The misidentifications perhaps had their basis in the fact that *serissima* was first described as a variety of *S. lucida* (Bailey 1887) and that Fernald (1904) suggested, "it might be sought with some confidence in Bennington Co., Vermont." The shininess and shape of the leaves of the two species are similar but not identical. The leaves of *S. serissima* are less shiny than those of *S. lucida*, and they are less acuminate than those of *S. lucida*, as illustrated by Argus (2010).

ADDITIONS FIRST REPORTED ELSEWHERE

Coursol (2007) reported *Lycopus laurentianus* Rolland-Germain from northern Lake Champlain in Vermont, as well as neighboring Québec and New York. This taxon was previously thought to have been endemic to shoreline habitats along the St. Lawrence River, and the Lake Champlain populations are among the first reported in the United States (in the same paper, Coursol also reported it from Maine). It differs from *L. americanus* Muhl. especially in the collar of spongy tissue that more or less rings the adaxial face of the nutlet which, in *L. laurentianus*, is reduced to a narrow rim, as well as characters of the leaf and the stem. Coursol and co-investigator S. Bailleul annotated specimens (at MT and VT) from Franklin, Grand Isle, and Chittenden Counties.

Pace and Cameron (2017) revised the *Spiranthes cernua* L. complex, adding two species to the state of Vermont, the newly described *Spiranthes arcisepala* M.C. Pace and the newly recognized *Spiranthes incurva* (Jenn.) M.C. Pace. At the same time, they excluded *Spiranthes cernua* s.s. from Vermont. *Spiranthes arcisepala* is similar to *S. cernua* and differs in several cryptic features including downward-arching sepals; specimens were cited from Franklin and Bennington Counties. *Spiranthes incurva* is of hybrid origin, with *S. cernua* and *S. magnicamporum* Sheviak as progenitors; its lateral sepals are often ascending. Pace and Cameron (2017) cited specimens from Franklin, Orleans, Windham, and Windsor counties.

Patel et al. (2019) described a new species, *Phegopteris excelsior* Patel & Gilman, that may be relatively common in Vermont. This species is much like a very robust *P. connectilis* (Michx.) Watt in appearance, with some fronds equaling in size the large fronds of *P. hexagonoptera* Fée. First hypothesized by Mulligan et al. (1972) as a hybrid between apogamous triploid *P. connectilis* and sexual diploid *P. hexagonoptera*, it is an apogamous tetraploid. Patel et al. (2019) found that while it is of hybrid origin, *P. hexagonoptera* is not involved. Although *P. connectilis* is a likely progenitor, a second progenitor has not been identified. It occurs from Nova Scotia to New York and is a species of forested habitats, often near streams or near, but not within, wetlands. In Vermont, it is known from Orleans, Caledonia, Washington, and Bennington Counties.

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A NEW COMBINATION IN *BARBILOPHOZIA* FOR *LOPHOZIA HYPERBOREA* SUBSP. *HELOPHILA* (SCAPANIACEAE, MARCHANTIOPHYTA) OF GREENLAND, WITH MACROEVOLUTIONARY JUSTIFICATION

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ABSTRACT

A new combination in the hepatic genus *Barbilophozia* is made for a subspecies of *Neoorthocaulis* (Scapaniaceae) to fit the conservative classification being used for the Flora of North America. Justification is given for avoiding names generated in new molecular classifications.

Volume 29 is the prospective volume of hepatics and hornworts for the FNA Editorial Committee (1993+). The genus *Barbilophozia* Loeske has presented a problem in classification. Rather than following the modern classification for the North American taxa proposed by Stotler and Crandall-Stotler (2017), which recognizes several segregate genera associated with *Barbilophozia* based on recent molecular work by many authors, the older, more inclusive genus is retained for Volume 29. A new combination is required for this conservative classification, which avoids using the molecularly based new genus *Neoorthocaulis* L. Söderstr., De Roo, & Hedd. Justification for this is presented in the discussion section below.

Barbilophozia hyperborea subsp. **helophila** (R.M. Schust. & Damsh.) R.H. Zander, **comb. nov.**
Basionym: *Lophozia hyperborea* subsp. *helophila* R.M. Schust. & Damsh., Phytologia 63: 325. 1987. *Neoorthocaulis hyperboreus* subsp. *helophilus* (R.M. Schust. & Damsh.) Stotler & Crandall-Stotl., Ann. Missouri Bot. Gard. 102: 659. 2017.

Barbilophozia hyperborea subsp. *helophila* is restricted to southern Greenland. It is distinguished from the typical subspecies by a red cast to the plants, smaller underleaves, and presence of gemmae.

A return to the classical concept of *Barbilophozia* is justified by the uncertainty associated with molecular systematics as nowadays practiced. The genus *Neoorthocaulis* was established by Söderström et al. (2010) to reflect recent molecular studies (Vilnet et al. 2007, 2008, 2010) of the *Lophozia* relationship among Scapaniaceae. This work distinguished *Barbilophozia* sensu stricto from the segregate genera *Orthocaulis* H. Buch, *Neoorthocaulis, Schljakovia* Konstant. & Vilnet, and *Schjakovianthus* Konstant. & Vilnet. The molecular studies are here considered negatively biased for the following reasons:

(1) Clades do not model evolution, which is serial, that is, species to species. Clades model series of sets of traits giving rise dichotomously to further split sets of traits, which is not a process in nature, but is a form of cluster analysis. A more realistic model is the dissilient genus concept (Zander 2013: 92, 2018: 170) of descendant species radiating from a central more generalized progenitor, a key organizing principle of macroevolutionary systematics (Zander 2019a).

(2) Metadata reviews (Zander 2019b, c) of molecular systematics studies of mosses in the family Pottiaceae, published by various phylogeneticists, have demonstrated that molecular races are common in species and that they are often molecularly paraphyletic such that any two OTUs within an average of 4.5 nodes has a good chance of one being a direct descendant of the other. Thus, sister

group distribution in a molecular cladogram is highly uncertain within a rather broad topological range. The same appears to be true for hepatics, with examples of multiracial species in the study of Vilnet et al. (2008), which revealed much infraspecific cladistic structure (serial branching), including species-level paraphyly.

(3) Molecular traits are sometimes cited as confirming molecular clades. This presents the statistical problem of multiple testing. A thorough search will usually find some traits that appear to concentrate within a particular molecular clade, usually polythetically (traits partially applicable but in total overlapping among all species). Morphological traits must stand on their own to corroborate molecular results or be considered random coincidences. Thus, there must be demonstrated no reasonable alternative to the putative morphological clustering. Bonferroni correction for multiple tests would be (Zander 2013: 113) to split the alpha in half if there were two morphological alternatives (selected as in flipping a coin), only one of which supports the molecular. This means that the statistical support needed for non-critical applications would be, not 0.94 BPP, but 0.97 BPP for the molecular results. Problematically, the morphological alternative may instead be similar to the classical, quite different clade structure, and with excellent Bayesian support through Shannon-Turing analysis (Zander 2018: 35, 173). In this case a Bayes factor method (Zander 2018: 39) must be used instead, which splits the total support, that is, provides about 0.50 BPP for both morphological and molecular concepts of relationships. The negative biases one and two given above argue for retaining the morphologically based classification.

Until the three objections made here are addressed, classical taxonomic name combinations should be preferred to radical new and different distributions of species into molecularly based genera.

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Sorrie, B.A. 2020. *Eremochloa ophiuroides* (Poaceae) — Distribution and collection chronology in the United States. Phytoneuron 2020-18: 1–7. Published 28 February 2020. ISSN 2153 733X

EREMOCHLOA OPHIUROIDES (POACEAE) — DISTRIBUTION AND COLLECTION CHRONOLOGY IN THE UNITED STATES

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ABSTRACT

The east Asian grass *Eremochloa ophiuroides* was introduced to the United States as far back as the 1920s. Specimen data indicate that it was originally grown in agronomy plots, forestry plantations, and Soil Conservation Service Experiment Stations in several states. Soon after, it entered the horticultural trade and was planted in lawns; thus began a period of slow spread in the southeastern USA. The pace of spread increased in the 1980s and was augmented by use in roadside seeding projects.

Centipede grass (*Eremochloa ophiuroides* (Munro) Hackel), native to southeastern Asia, was introduced to the United States as a lawn grass, according to Hitchcock and Chase (1951). It is a perennial, long-stoloniferous, mat-forming grass with short, distichous leaves held parallel to the ground. Inflorescences are deep red or red-brown, spikelike, and held erect on slender stalks (Figures 1-3).

My interest in this species comes from the fact that it was a late addition to the North Carolina flora, just as the Manual of the Vascular Flora of the Carolinas (Radford, Ahles, & Bell 1968) went to press in 1968. The authors recorded it from only two counties in each state. Since then, however, it has spread widely and rapidly in both states and now is one of the most abundant species of mown roadsides. In this paper I track the chronology of its spread in the USA and suggest its original introduction points.

Approximately 220 specimens of centipede grass were examined online at SERNEC (2019) and the following data extracted: state, county, habitat, date, collector and number, and repository. Additional counties of occurrence were taken from various state atlases and from BONAP (Kartesz 2019). Distribution maps were prepared utilizing a program developed by Mike Lee (2019).

Results

Map 1 displays the overall distribution of centipede grass in the USA. Maps 2-5 display decade-by-decade spread of the species, as reflected by specimen collecting dates. Centipede grass is now naturalized on the Coastal Plain from southeastern Virginia to southern Florida, eastern Texas, and southern Arkansas; scattered records exist inland to western South Carolina, eastern Tennessee, northeastern Alabama, north-central Arkansas, and southeastern Missouri (Map 1). It is disjunct to western Massachusetts.

Locality data for the earliest collections per state are given here.

Alabama: 1958, roadside in Lillian, Baldwin Co. 1959, agronomy farm, Auburn University, Lee Co. 1969, near forestry plots, Auburn University, Lee Co.

Florida: 1925, introduced at Belle Glade Experiment Station, Palm Beach Co. 1932, no habitat, Fern Park, Seminole Co. 1934, cultivated, no locale, Orange Co. 1934, oak woods, Highlands Hammock, Highlands Co.

Georgia: 1937, forest plantation #20, N of Quitman, Brooks Co.

Louisiana: 1967, roadside at railroad crossing, St. Tammany Par.

Massachusetts: 1980, back yard disturbed area, Franklin Co.

Mississippi: 1951, planted in lawn, Adams Co. 1957, lawn in Lucedale, George Co.

Missouri: 1997, cultivated grass in lawn, Clearmont Street, Poplar Bluff, Butler Co.

North Carolina: 1941, planted and grown in nursery at Soil Conservation Service, Chapel Hill, Orange Co. 1967, Methodist College campus lawn, Cumberland Co.

South Carolina: 1943, introduced to yard, Hartsville, Darlington Co. 1961, roadside CR 27 at CR 23, Lancaster Co.

Tennessee: 1956, 204 Gadd Road, Chattanooga, Hamilton Co. 1960, cultivated at University of Tennessee Farm, Knox Co.

Texas: 1947, 3610 Windsor Road, Austin, Travis Co. 1968, lawn at Meadow Lane, Bryan, Brazos Co.

Virginia: 1995, parking lot, False Cape State Park, Virginia Beach City.

From the above it can be seen that centipede grass was indeed planted early on in lawns. However, other means of introduction are noted, and these often are the oldest in a given state. The earliest Georgia record (1937) is from a forestry plot, as is a 1969 specimen from Alabama. An even earlier specimen from Alabama (1959) was collected from a university agronomy farm, as was a 1960 specimen from Tennessee, and the earliest specimen from North Carolina (1941) was from a Soil Conservation Service nursery, just off campus from UNC-Chapel Hill. Finally, the first Florida specimen (1925) was collected in an Experiment Station in Palm Beach County.

From the available historical record, it would appear that *Eremochloa ophiuroides* was first grown in various agronomy farms, experiment stations, and forestry plantations, perhaps as a means of "testing" its suitability to local conditions. Then it soon became available to private landowners, which increased the distribution of the species. As far as the specimen record indicates, geographical spread appears to have been slow through the 1950s (Map 2), moderate through the 1970s (Map 3), and rapid in the 1980s and more recently (Maps 4-5).

One final means of spread, not mentioned above, is that of state departments of transportation, or highway departments — deliberate planting on major highway medians and shoulders and on mown sides of secondary roads. For example, centipede grass has been part of roadside seed mixes in North Carolina since the late 1980s (R. Badgett, NCDOT, pers. comm.). It is highly likely that recent use (since the 1980s) of centipede grasss in seed mixes has augmented the rapid spread in North Carolina and perhaps other states.

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A study of this nature could not have been done without the countless hours of specimen data entry into the SERNEC website; thanks to herbarium managers and data entry people. Thanks to John Kartesz for his many years of critical work in maintaining the BONAP database. I thank Mike Lee for developing the county-level mapping program.

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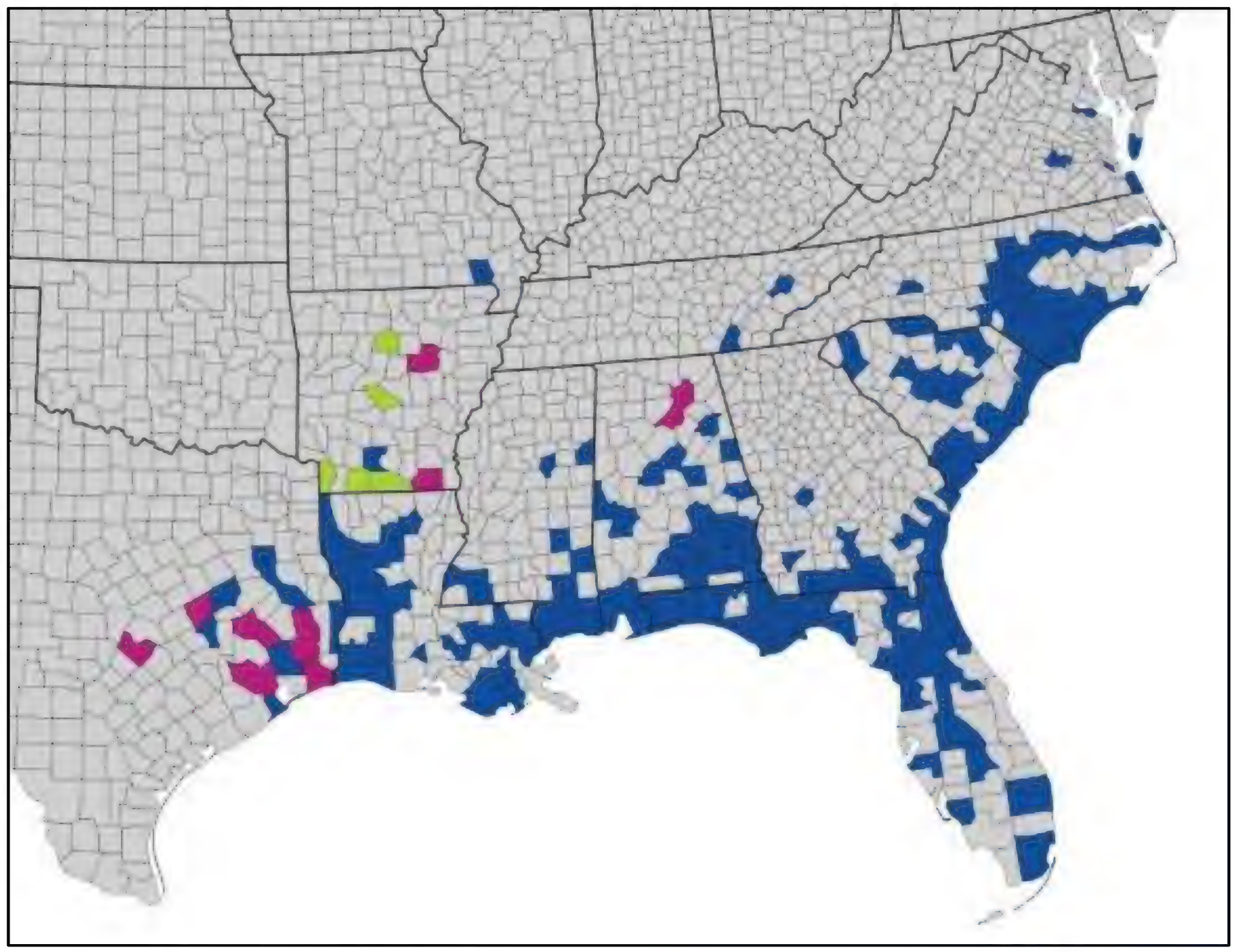
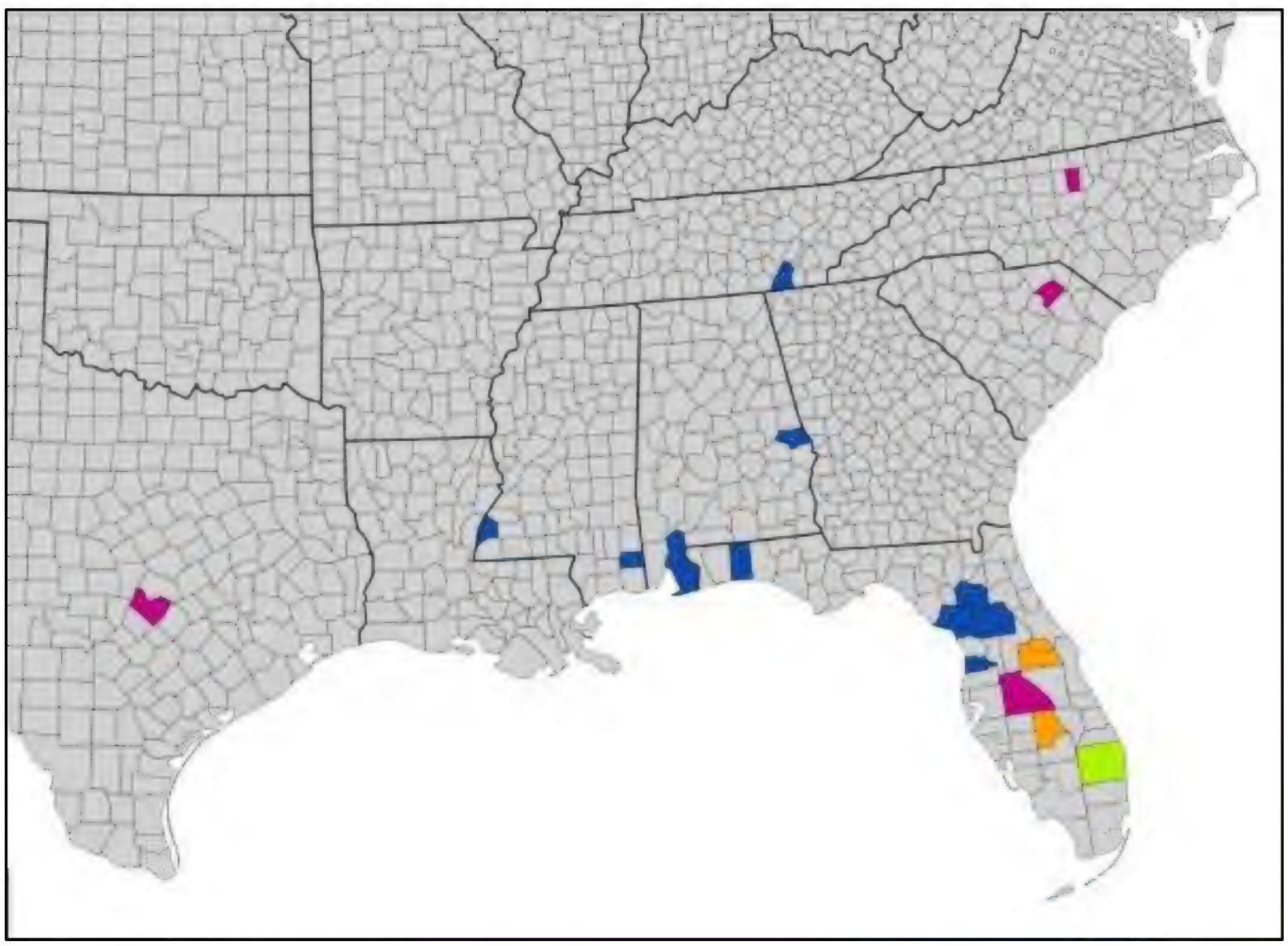
Figure 1. *Eremochloa ophiuroides*. Large population dominant on open roadside. Moore Co., North Carolina.

Figure 2. *Eremochloa ophiuroides*. Flowering culms. Moore Co., North Carolina.

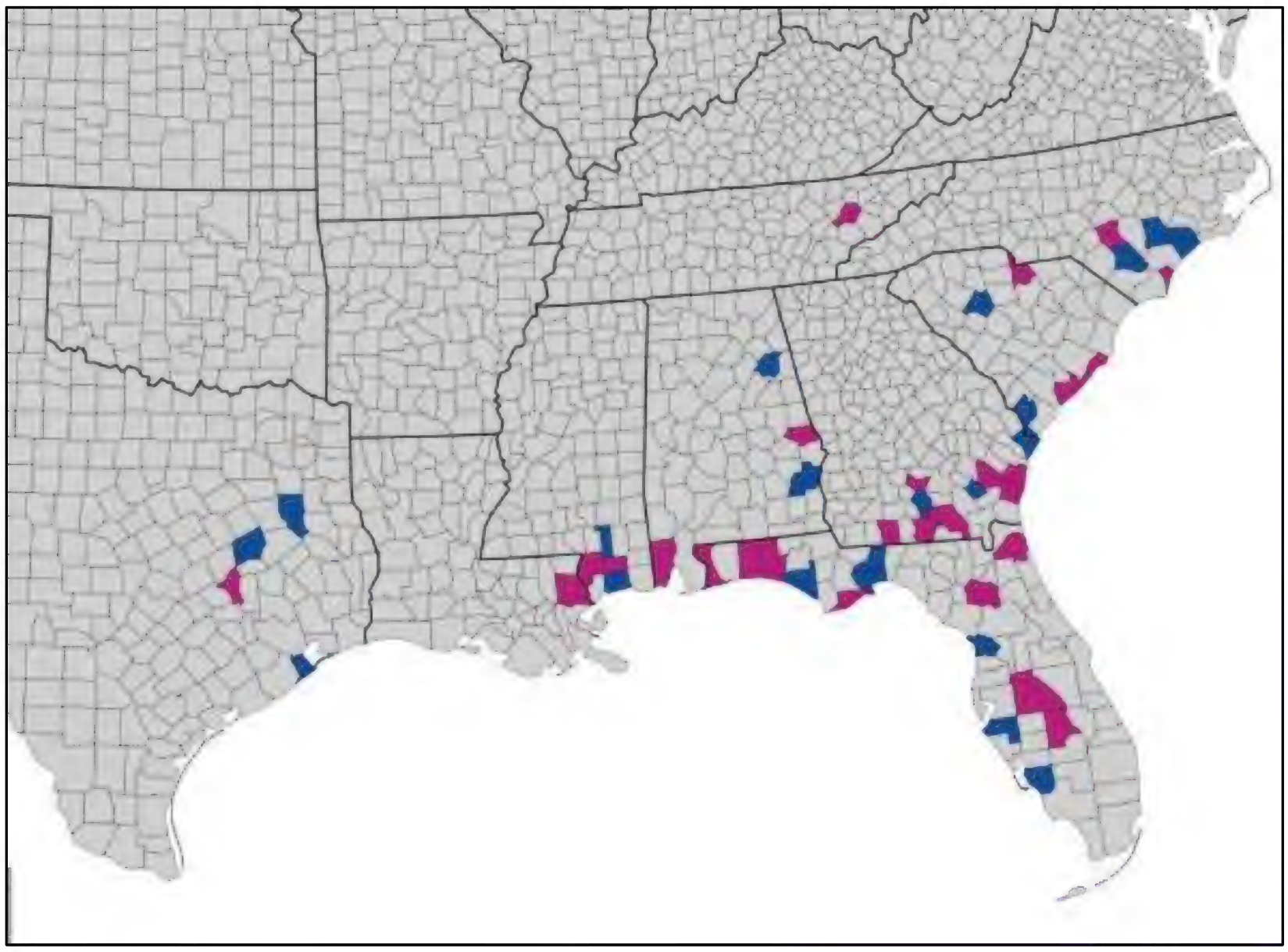
Figure 3. *Eremochloa ophiuroides*. Prostrate stem and leaves. Moore Co., North Carolina.



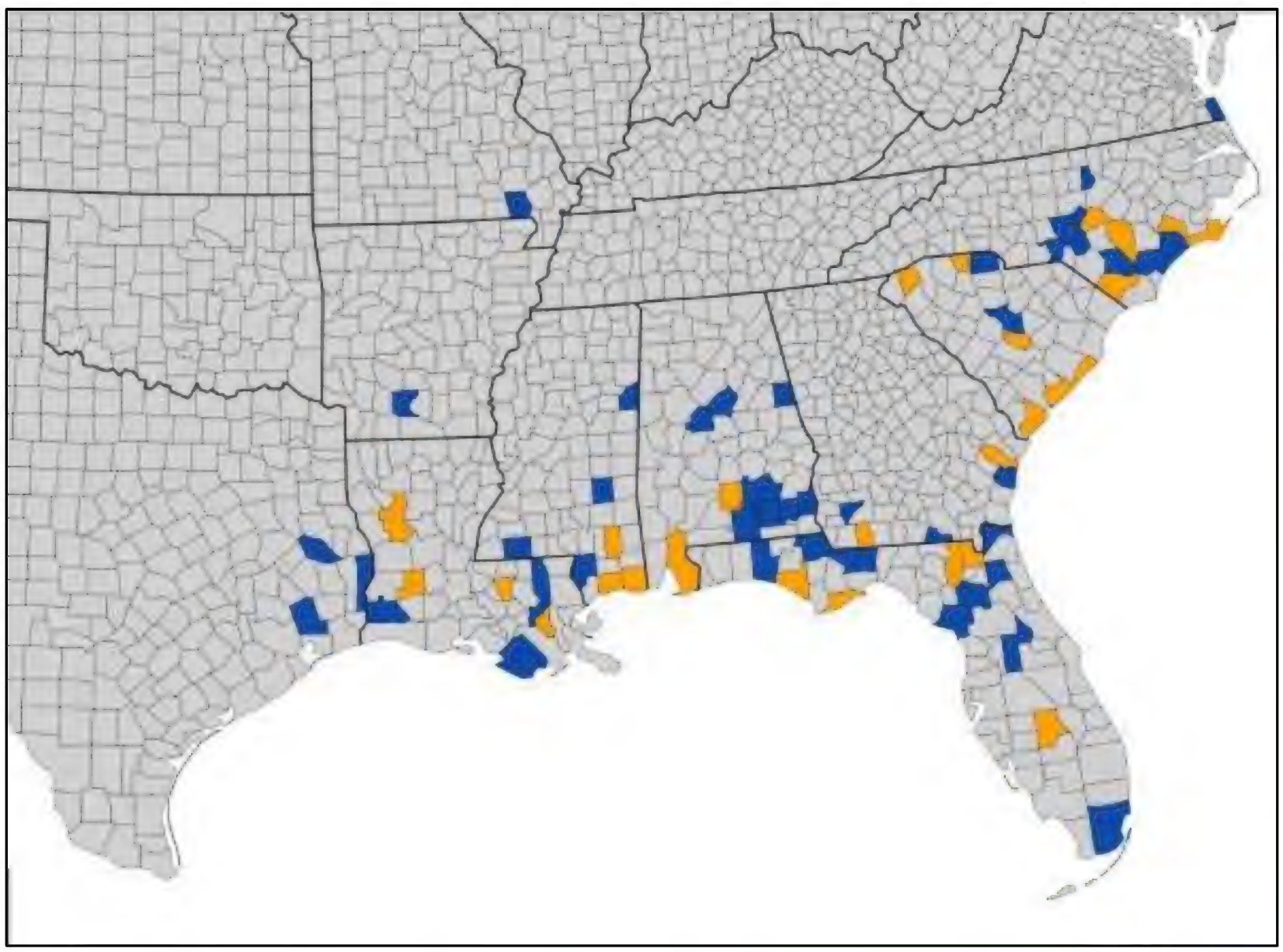
Map 1. Distribution of *Eremochloa ophiuroides*. Blue = specimen record from herbaria or SERNEC. Green = state plant atlas. Red = BONAP map.



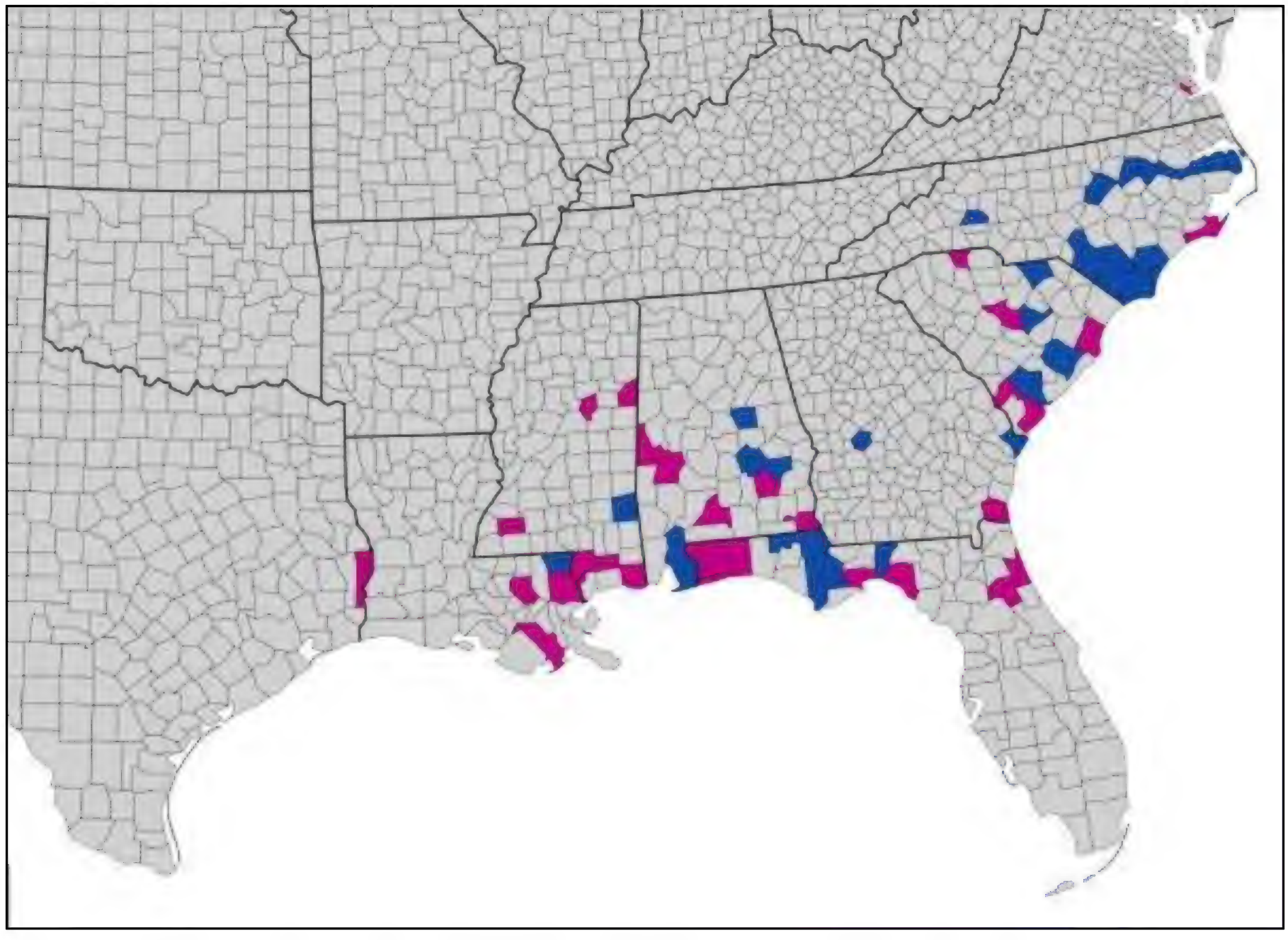
Map 2. Collections of *Eremochloa ophiuroides*, 1920-1959. Green = 1920s. Orange = 1930s. Red = 1940s. Blue = 1950s.



Map 3. Collections of *Eremochloa ophiuroides*, 1960-1979. Red = 1960s. Blue = 1970s.



Map 4. Collections of *Eremochloa ophiuroides*, 1980-1999. Orange = 1980s. Blue = 1990s.



Map 5. Collections of *Eremochloa ophiuroides*, 2000-2019. Red = 2000s. Blue = 2010s.

Ahlquist, T.K. and M.A. Vincent. 2020. *Trifolium hickeyi* (Fabaceae), a new species in the *T. amabile* complex from Mexico and Guatemala. Phytoneuron 2020-19: 1–5. Published 28 February 2020. ISSN 2153 733X

TRIFOLIUM HICKEYI (FABACEAE), A NEW SPECIES IN THE *T. AMABILE* COMPLEX FROM MEXICO AND GUATEMALA

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ABSTRACT

Trifolium hickeyi Ahlquist & Vincent, **sp. nov.**, is described from central and southern Mexico, from the states of Chiapas, Jalisco, México, Michoacán, Oaxaca, Puebla, and Veracruz, and from Guatemala. It can be distinguished from other members of the *Trifolium amabile* complex by a number of vegetative and reproductive characters much larger in size than those observed in other species. The most notable are the very long peduncles, over 8 cm long, and the glabrous ovaries.

Within *Trifolium amabile* Kunth, Zohary and Heller (1984) recognized five varieties in their monograph of the genus (var. *amabile*, var. *hemsleyi* (Lojac.) Heller & Zohary, var. *longifoliolum* Hemsl., var. *mexicanum* (Hemsl.) Heller & Zohary, and var. *pentlandii* Ball). Research by Ahlquist (2012) did not support recognition of these varieties, which had also been questioned by Zohary and Heller as well as McVaugh (1987), who questioned the circumscriptions of the Mexican taxa. Analyses of the *T. amabile* complex have revealed a new species, *T. hickeyi* (Fig. 1), which is similar to *T. rhombeum* S. Schauer (*T. amabile var. mexicanum* of Zohary & Heller). It is an exceptional species, growing to a height of 8 dm or more, with large leaflets between 1.4 cm and 4.6 cm long, stipules ranging from 2 cm and 4 cm long, peduncles measuring over 8 cm long, and glabrous ovaries. The new species is described and illustrated below.

TRIFOLIUM HICKEYI Ahlquist & Vincent **sp. nov.** **TYPE**: **MEXICO**. **Michoacán**. Morelia, Rincón prise d'eau, 16.698º, -101.187º, 1950 m, 14 Apr 1910, *G. Arsène 5483* (holotype: ILL!; isotypes: BM!, GH!, NY!). Figure 1.

Plants perennial. **Roots** large, woody, 3.3–11.8 mm in diameter. **Stems** prostrate to decumbent or ascending, 1.2–7.8+ dm long, 1–4.5 mm in diameter, internodes and nodes glabrous to moderately pubescent. **Leaves** trifoliate, ± uniform in size throughout. **Stipules** narrowly triangular to triangular, 1.95–3.75 × 0.2–0.85 cm, glabrous adaxially and abaxially, margins entire to weakly serrate, glabrous–sparsely pubescent, apices acute. **Petioles** 0.55–10.7 cm long, glabrous to sparsely pubescent. **Petiolules** 0.5–4 mm long, glabrous to moderately pubescent. **Leaflets** lanceolate-elliptic, occasionally rhombic, glabrous adaxially, glabrous to moderately pubescent along midribs abaxially, glabrous to sparsely pubescent abaxially on outer halves of lateral leaflets, bases acute, margins variably serrate, often with short, straight teeth alternating with larger, curved teeth, glabrous to sparsely pubescent, apices rounded to acute, weakly mucronulate, terminal leaflets 1.35–4.6 × 0.55–1.85 cm. **Peduncles** 7.6–21.1 cm × ≤2 mm, glabrous to moderately pubescent. **Inflorescences** axillary, racemose to umbellate, 0.95–2.6 × 1.6–2.6 cm. **Flowers** 17–50, each subtended by a linear triangular

bract, in 2–5 whorls. **Pedicels** 0.7–3.6 mm long, glabrous to sparsely pubescent. **Calyx** 3.9–7.4 mm long, tubes 2.6–4.1 mm in circumference, glabrous to sparsely pubescent, lobes narrowly triangular, 3–6 × <1 mm, glabrous to sparsely pubescent abaxially, margins entire, sparsely to moderately pubescent, apices acuminate. **Petals** white to yellowish white. **Banner petals** obovate, 6–9.6 × 3.8–6.3 mm. **Wing petals** 5.5–8.2 mm long, asymmetrically clawed, claws 1.1–2.1 × ≤0.5 mm, laminae spatulate, 4.2–6.2 mm long, 1.7–2.9 mm wide at widest point, 0.9–1.4 mm wide at narrowest point, bases shortly auriculate to truncate, auricles acute, margins entire, apices rounded. **Keel petals** 4.5–6.6 mm long, asymmetrically clawed, claws 1.4–2.4 × ≤0.6 mm, laminae spatulate, 3–4.2 mm long, 1.5–2 mm wide at widest point, 0.9–1.5 mm wide at narrowest point, bases truncate, margins entire, apices rounded. **Stamens** diadelphous, connate filaments 3.7–5.6 × 1.1–1.6 mm, fused for 50–70% of their length, free filaments 2.1–4.4 × ≤0.2 mm. **Pistils** sessile, ovaries 1.3–3.5 × 0.4–1.6 mm, glabrous, styles 1.7–2.9 × ≤0.3 mm, glabrous, ovules 2. **Legumes** laterally compressed, 3.3–5.2 × 1.9–2.7 mm. **Seeds** 2, mitten-shaped, light brown to dark brown, occasionally dark-speckled, 1.7–2.2 × 1.2–1.6 mm.

Additional collections examined. **Guatemala**. **Chimaltenango**. Chichavac, 14.8º, -90.98º, 2550 m, flowers greenish white, Nov 1930, *Skutch 88* (MICH, US). **Huehuetenango**. Vicinity of San Mateo Ixtatán, Sierra de los Cuchumatanes, 15.8º, -91.4º, 3100 m, flowers dull whitish, 31 Jul 1942, *Steyermark 49895* (F, NY, US). **San Marcos**. San Pedro Sacatepéquez, Aldea Chamác, 14.969º, -91.756º, 2200 m, hierba prostrada, muy abundante, 26 Aug 1992, *Véliz 92.2418* (MO). **Mexico**. **Chiapas**. Laguna Jusnajav, 16 km NE of Comitán, 16.380º, -92.038º, 1758 m, 29 Aug 1945, *Alexander 1265* (MICH, NY). **Guanajuato**. Mpio. Acámbaro, La Cieneguilla, zona de cultivo, terreno plano, 21.075º, -100.175º, 1775 m, hierba abundante, 18 Aug 1985, *Rubio 69* (XAL). **Jalisco**. Sierra del Tigre, 2 mi NE of Mazamitla, gently sloping wet meadow-like areas in pine forest zone, 19.883º, -102.983º, 2100 m, abundant, mostly past flower, flowers cream color, 23 Sep 1952, *McVaugh 13186* (MICH). **México**. Mpio. Tepotzoltan, cerca de la Presa de Concepción, orilla de arroyo, 19.717º, -99.223º, 2400 m, flor blanquecina, 7 Aug 1966, *Rzedowski 22885* (ASU, MICH). **Michoacán**. Morelia, 19.7º, -101.2º, 1950 m, 1 Aug 1912, *Arsène 8323* (B, NY, P); Mpio. Villa Morelos, alrededores de El Fresno, orilla de una acequia, 20.026º, -102.882º, 2250 m, planta herbácea perenne, flores de color crema, 30 Aug 1987, *Rzedowski 44278* (MICH). **Oaxaca**. Ixlán de Juárez, E-facing slopes, mountains along Route 175, 12 km N of Ixlán de Juárez on road to Valle Nacional, in forest of pine and deciduous trees, open sun, gravelly soil, 17.439º, -96.474º, 2500 m, abundant, flowers white, 26 Jul 1956, *King 2043* (MICH); Mpio. Santiago Juxtlahuaca, senda hacia la torre de microondas de El Manzanal, entrada por Santa Rosa-San Miguel Cuevas, bosque de *Pinus-Quercus*, suelo café rocoso, 17.225333º, -98.054611º, 2225 m, hierba de 60 a 70 cm de alto, flor blanca, planta de regular abundancia, 12 Sep 1996, *Calzada 21326* (MO); Tlacolula, a 16 km al NNE de Díaz Ordaz, o sea a 6 km al S de Cuajimaloya, Distr. Tlacolula, veg. alterada de encinar, 17.070º, -96.4º, 2670 m, herbacea perenne, arrocetada, flores blancas con rosa, 7 Aug 1977, *Sousa 7822 et al.* (MICH, NY); 110 km by road S of Teotitlán on road to Oaxaca, oak forest, 16.2º, -96.6º, 2180 m, decumbent from taproot, flowers yellowish green, 11 Oct 1983, *Anderson 13019* (MICH); Cumbre de Ixtepec, 16.57º, -95.1º, 60 m, Sep 1942, *Liebmann 4928* (C, US). **Puebla-Oaxaca**. San Luis Tultitanapa, Cerro Verde, near Oaxaca, 18.1º, -97.3º, 1400 m, Jul 1908, *Purpus 3228* (GH, NY, US). **Puebla-Veracruz**. Orizaba, 19º, -97.2º, 4500 m, 1856, *Botteri 704* (NY, P).

Trifolium hickeyi is named in honor of mentor and colleague R. James Hickey, professor emeritus and former chair of the Department of Botany at Miami University.

Trifolium hickeyi is found primarily in central and southern Mexico in the states of Chiapas, Jalisco, México, Michoacán, Oaxaca, Puebla, and Veracruz, and in Guatemala (Fig. 2). It has been collected in oak-pine forests and on grassy slopes, wet meadows, ditches, and roadsides with gravelly to rocky soil; 1400–4500 meters in elevation.

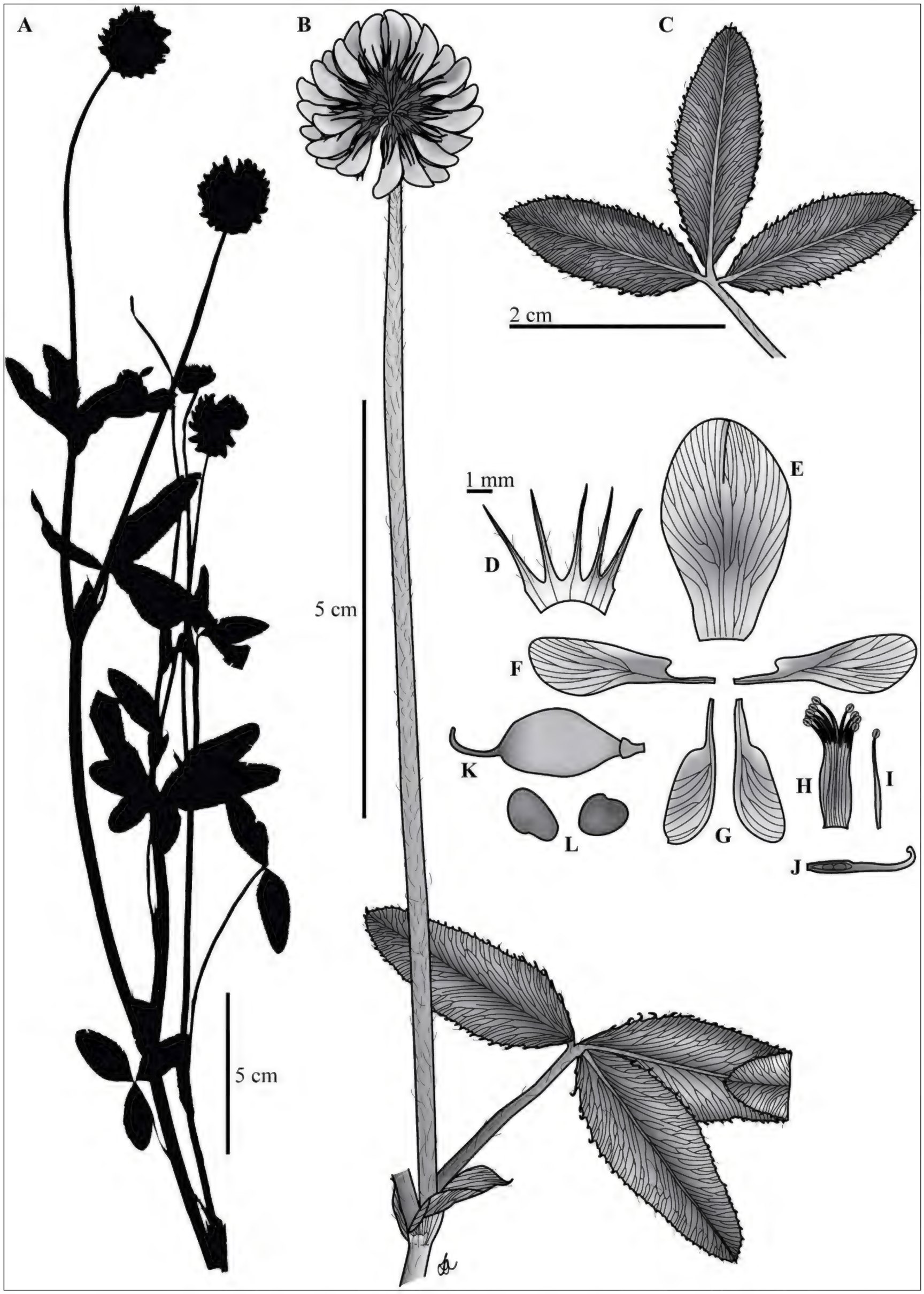

Figure 1. *Trifolium hickeyi* (from the holotype). A. Habit silhouette. B. Fertile branch. C. Abaxial leaf surface. D. Sepals. E. Banner petal. F. Wing petals. G. Keel petals. H. Connate stamens. I. Free stamen. J. Ovary. K. Legume. L. Seeds.

Figure 2. Distribution of *Trifolium hickeyi* in Mexico and Guatemala.

Trifolium hickeyi exhibits many characters observed in the *T. amabile* species complex, including a perennial life cycle, woody roots, and habit and pubescence characters. The new species differs from *T. rhombeum* as in the couplet below.

1. Stipules 8–17 mm long; peduncles 3–8 cm long; ovaries sparsely to densely pubescent ..... **Trifolium rhombeum**
1. Stipules 19–38 mm long; peduncles 7–21 cm long; ovaries glabrous ..... **Trifolium hickeyi**

Overall, *T. rhombeum* is rather pubescent — the ovaries are sparsely to densely pubescent distally and occasionally along the suture. The glabrous ovaries of *T. hickeyi* distinguish it from all other members in the *T. amabile* complex.

Trifolium hickeyi is identified by a number of vegetative and reproductive characters well outside of the size range of the other members of the species complex. Over 87% of the characters examined in this study in a student's t-test were significantly different at $\alpha=0.05$ when compared with *T. amabile* var. *amabile* (Ahlquist 2012). When compared with *T. rhombeum*, over 57% of characters were statistically significant at $\alpha=0.05$ (Ahlquist 2012).

Within *Trifolium hickeyi* there is a clinal grade from north to south in leaflet morphology. The specimens at the northern end of the range have rhombic leaflets similar to those of *T. rhombeum*; all other characters are consistent with the southern specimens of *T. hickeyi*.

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SINOPSIS DEL GÉNERO *MYROXYLON* (FABACEAE) EN COSTA RICA

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RESUMEN

Se presenta una sinopsis del género *Myroxylon* (Fabaceae) en Costa Rica. Se incluye un mapa de la distribución natural conocida de las dos especies del género (*M. balsamum* y *M. peruiferum*), anteriormente confundidas en el país. Se registra una nueva localidad donde crece silvestre *M. peruiferum* (cuenca del río Barranca, San Ramón, Alajuela). Se proporciona una clave de identificación y una lista de ejemplares de herbario examinados.

ABSTRACT

A synopsis of the genus *Myroxylon* (Fabaceae) in Costa Rica is presented. A map of the known natural distribution of the two species of the genus (*M. balsamum* and *M. peruiferum*, previously confused in the country), is included. A new locality where *M. peruiferum* grows wild is recorded (Barranca river basin, San Ramón, Alajuela). An identification key and a list of specimens examined are provided.

Fabaceae Lindl. (≡ Leguminosae Juss.), con cerca de 770 géneros y más de 19500 especies, es la tercera familia de angiospermas con mayor diversidad a nivel mundial (LPWG 2017). Actualmente, las fabáceas se clasifican en seis subfamilias (Caesalpinioideae DC., Cercidoideae LPWG, Detarioideae Burmeist., Dialioideae LPWG, Duparquetioideae LPWG y Papilionoideae DC.), siendo Papilionoideae (≡ Faboideae Rudd) la más diversa, con aproximadamente 503 géneros y 14000 especies descritas (LPWG 2017). Las tribus de esta subfamilia (e.g., Dalbergieae Bronn ex DC., Dipteryxeae Polhill, Sophoreae Spreng. ex DC., Swartzieae DC.) son grupos polifiléticos cuya filogenia aún no se ha resuelto (Choi & Choi 2017).

Myroxylon L.f. (Fabaceae, Faboideae), nombre conservado contra *Toluifera* L., es un género neotropical clasificado en Sophoreae. De Candolle (1825) lo trató como una sección de *Myrospermum* Jacq., mientras que Klotzsch (1843) lo elevó de nuevo al rango de género. Baillon (1870) restituyó el nombre *Toluifera*, pero Harms (1908) retomó el nombre *Myroxylon* y reconoció dos especies y tres variedades [*M. balsamum* (L.) Harms var. *balsamum*, *M. b.* var. *pereirae* (Royle) Harms, *M. b.* var. *punctatum* (Klotzsch) Harms y *M. peruiferum* L.f.]; criterio que siguió Rudd (1968). Sin embargo, Sartori et al. (2015) reconocen únicamente dos especies (*M. balsamum* y *M. peruiferum*) y ninguna variedad.

Standley (1938) registró por primera vez la presencia de *M. balsamum* en Costa Rica; desde entonces se consideró que esta era la única especie del género en el país (Zamora 2010). Este criterio cambió al confirmarse la presencia de *M. peruiferum* en sitios ubicados al suroeste del Valle Central, junto con la comprobación de que todos los ejemplares de *M. peruiferum*, en los herbarios CR, JVR y USJ, habían sido identificados como *M. balsamum* (Aguilar-Sandí 2019). Lo cual condujo a confundir ambas especies, registrándose *M. balsamum* en sitios donde se encuentra *M. peruiferum* (Fournier et al. 1985; Quesada et al. 1997; Jiménez 1998; Zamora 2010; Jiménez et al. 2011). Esta sinopsis tiene por objetivo actualizar el conocimiento sobre el género *Myroxylon* en Costa Rica.

Métodos. Se estudiaron las colecciones de los herbarios CR, JVR y USJ. A partir de este material se elaboró la clave dicotómica, en este proceso también se utilizaron muestras frescas. Los

datos sobre fenología se obtuvieron de las etiquetas de los ejemplares de herbario. En noviembre de 2019 y enero de 2020 se hicieron recolectas de *M. peruiferum* en dos sitios ubicados en la cuenca del río Barranca en San Ramón de Alajuela. Con esta información, y con la ya disponible en herbarios, se confeccionó el mapa de distribución de ambas especies. Adicionalmente, se hicieron comparaciones morfológicas con imágenes digitales de ejemplares de los herbarios EAP y TEFH.

MYROXYLON L.f. Suppl. Pl. 233. 1781 [1782]. (*Nom. cons.*). *Toluifera* L. Sp. Pl. 1: 384. 1753.
TIPO: *Myroxylon peruiferum* L.f.

Distribución. Desde el sur de México hasta el norte de Argentina y Brasil.

Etimología. El nombre significa "madera con olor a bálsamo". Está formado de los términos griegos *myron* (μύρον: bálsamo, ungüento, esencia) y *xylon* (ξύλον: madera) (Pabón de Urbina 2006).

Notas. Las dos especies del género están presentes de forma silvestre en Costa Rica (Fig., 1). Ambas son árboles de 15–50 m de altura, con peridermis grisácea-blancuzca, lenticelada, lenticelas dispuestas en hileras longitudinales, corteza resinosa-aromática, estípulas deciduas, hojas imparipinnadas, alternas, folíolos alternos, en ocasiones con lámina ondulada, siempre con puntos y rayas translúcidos, inflorescencias racemosas, terminales o axilares, flores papilionáceas, frutos samaroides, con 1 o 2 semillas reniformes. En Sartori et al. (2015) se incluyen descripciones morfológicas detalladas tanto del género como de las especies.

Clave para las especies de *Myroxylon*

1. Lámina de los folíolos 4.5–8.5(–12.5) × 2–4.5 cm, ápices de los folíolos acuminados a largamente acuminados, cáliz lobulado, cámara seminífera subglobosa (en frutos maduros), semillas de testa lisa ..... **Myroxylon balsamum**
1. Lámina de los folíolos 3–4.5(–7.5) × 1.5–3 cm, ápices de los folíolos retusos a acuminados, cáliz sin lóbulos, cámara seminífera aplanada (en frutos maduros), semillas de testa rugosa ..... **Myroxylon peruiferum**

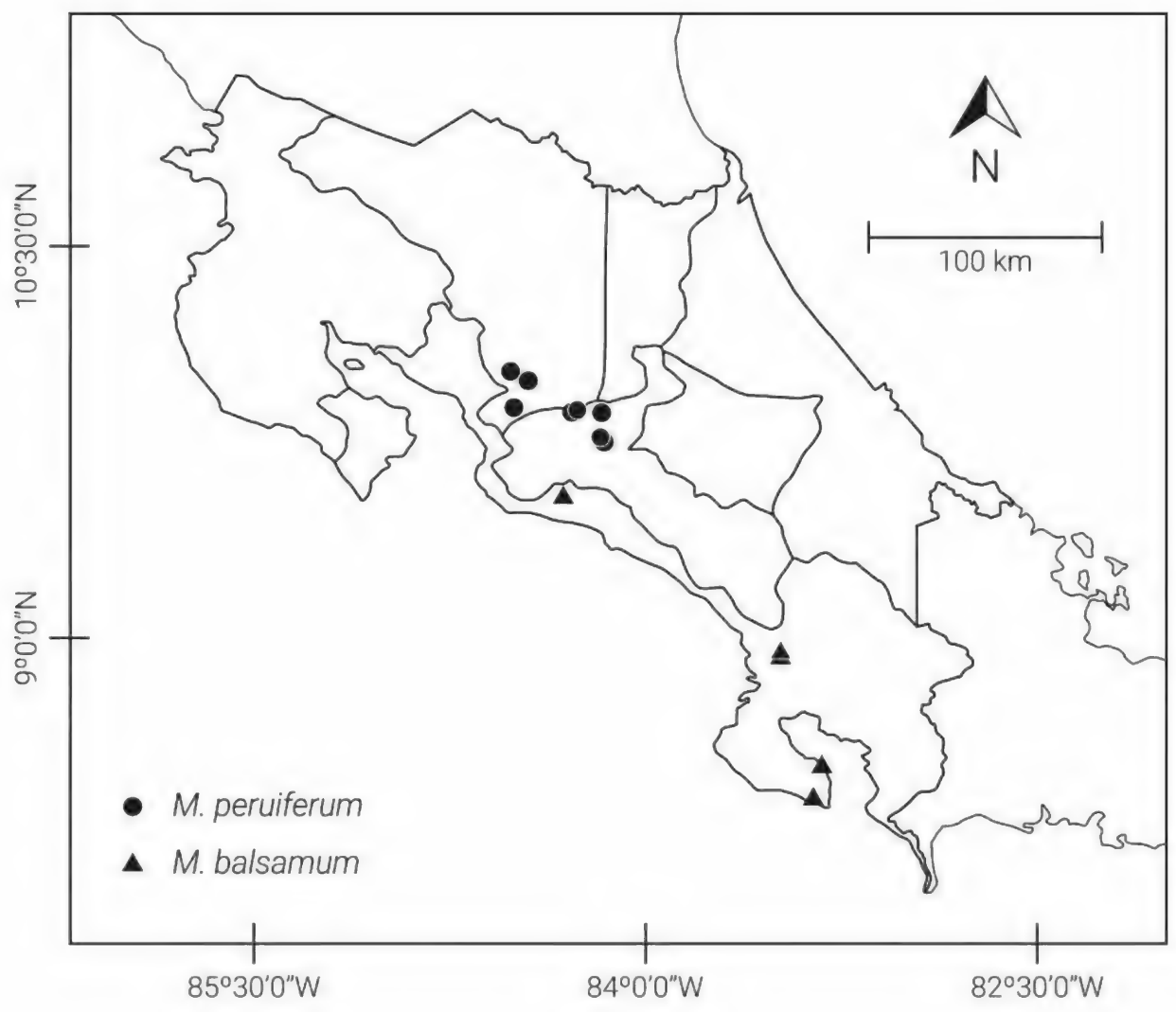

Figura 1. Distribución natural conocida de las especies del género *Myroxylon* en Costa Rica.

MYROXYLON BALSAMUM (L.) Harms, Notizbl. Königl. Bot. Gart. Berlin 5 (43): 94. 1908. *Toluifera balsamum* L., Sp. Pl. 1: 384. 1753. *Myroxylon balsamum* (L.) Harms var. *balsamum*, Notizbl. Königl. Bot. Gart. Berlin 5 (43): 94. 1908. **NEOTIPO** (Sartori et al. 2015): **Venezuela**. Puerto Cabello. s.d., *Goering 3/69* (K; isoneotipo: NY02256475). Fig. 2.

Myroxylon toluiferum Kunth, Nov. Gen. Sp. 375. 1824. *Myrospermum toluiferum* (Kunth) DC., Prodr. 2: 95. 1825. **LECTOTIPO** (Sartori et al. 2015): **Colombia**. Turbaco, s.d., *Bonpland 1405* (P670270).

Myroxylon punctatum Klotzsch, Getreue Darstell. Gew. 14: 12. 1843. *Myrospermum punctatum* (Klotzsch) Walp., Repert. Bot. Syst. 1 (5): 805. 1843. *Myroxylon balsamum* var. *punctatum* (Klotzsch) Harms, Notizbl. Königl. Bot. Gart. Berlin 5 (43): 97. 1908. **LECTOTIPO** (Sartori et al. 2015): **Perú**. Chicoplaya, Pozuzo, s.d., *Pavon* s.n. (G00404304).

Myrospermum pereirae Royle, Man. Mat. Med. 2: 414. 1853. *Myroxylon pereirae* (Royle) Klotzsch, Bonplandia 5(17): 274. 1857. *Toluifera pereirae* (Royle) Baill., Hist. Pl. 2: 383. 1870. *Toluifera balsamum* var. *pereirae* (Royle) Baill., Traite. Bot. Med. 676. 1883. *Myroxylon balsamum* var. *pereirae* (Royle) Harms, Notizbl. Königl. Bot. Gart. Berlin 5 (43): 95. 1908. **LECTOTIPO** (Sartori et al. 2015): **Guatemala**. s.d. *Skinner* s.n. (K).

Myroxylon hanburyanum Klotzsch, Bonplandia 5(17): 275. 1857. **LECTOTIPO** (Sartori et al. 2015): **America do sul**. Rio Amazonas, Maranon, s.d., *Warszewicz* s.n. (BM53843).

Distribución. Vertiente pacífica, 0–850 m, en sitios comprendidos en las regiones climáticas Pacífico Central y Pacífico Sur, con estación lluviosa prolongada, precipitación anual de 2000 a 5000 mm y temperaturas de 21 a 32 °C (Maldonado 2005). Provincia de Puntarenas, cantones de Parrita, Golfito y Osa.

Fenología. Especie perennifolia. Floración de enero a junio, fructificación de abril a octubre.

Nombres comunes. Bálsamo, chirraco, chirraca, sándalo.

Usos. La resina extraída del tronco, conocida como bálsamo negro o bálsamo del Perú, se ha utilizado desde la época precolombina. Las personas dedicadas a su extracción son conocidas como balsameros (Revene 2007). En la actualidad, esta actividad se realiza principalmente en El Salvador, país con una tradición balsamera centenaria (Martínez et al. 2015). La extracción se lleva a cabo de forma artesanal; para los detalles ver Fuentes (1993). En la época colonial, España enviaba cargamentos de resina producida en El Salvador a los puertos de Callao en Perú, y de allí a Europa, por esta razón se popularizó el nombre "bálsamo del Perú", tanto para la resina como para los árboles que la producen (Standley 1928). La resina del bálsamo se utiliza en la fabricación de jabones, barnices, pomadas, aromatizantes, desodorantes, cosméticos, perfumes e inciensos. También se ha utilizado con fines medicinales, para el tratamiento del reumatismo, la tos y los dolores de estómago, así como antihelmíntico, expectorante y cicatrizante (Revene 2007; Martínez et al. 2015). En el siglo XVI, el Vaticano promovió el uso de esta resina en las ceremonias religiosas (Standley 1928).

No se encontraron registros de una cultura balsamera en Costa Rica. Sin embargo, sí hay información sobre el uso de la resina en medicina tradicional (Pittier 1957; Núnez 1978) y sobre la existencia de explotación maderera (Jiménez et al. 2011). La madera de esta especie es aromática, resistente a la pudrición y muy pesada (peso específico aprox. 0.72 g/cm^3); se ha utilizado en ebanistería, lutería (guitarras, teclas de marimba), construcción de edificaciones (vigas, pisos, columnas) y en durmientes para línea de ferrocarril (Jiménez et al. 2011; Martínez et al. 2015). El duramen adquiere un tono rojizo al pulirlo y barnizarlo (Fig., 2, D).

Estado de conservación. Especie considerada en peligro de extinción en Costa Rica (Jiménez 1998) y vedada mediante el Decreto Ejecutivo Nº 25700-MINAE (Aguilar-Sandí 2019). Sin embargo, está clasificada como no amenazada en Catalogue of Life (2019) y no está incluida en la Lista Roja (UICN 2019).

Ejemplares examinados seleccionados. COSTA RICA. [**Alajuela**]. Cantón Orotina, 17 jun. 1938 (fr.), Orozco s.n. (USJ 922) [cultivado]. **Guanacaste**. Cantón La Cruz, Parque Nacional Guanacaste, Cuenca del Sapoá, Sector Maritza, 10°57'38.6400"N, 85°29'42.8540"W, 600 m, 02 may. 2000, Acosta 1111 (CR); Parque Nacional Guanacaste, Estación Maritza, 10°57.6'N, 85°29.6'W, 06 jul. 1989, II INBio 150 (CR). **Puntarenas**. Cantón Golfito, [Península de Osa], [Puerto Jiménez], Piro, 08°25'00"N, 83°20'35"W, 100 m, 14 oct. 1991, Aguilar 532 (CR); Puerto Jiménez, sendero La Piedra, 08°32'30"N, 83°18'30"W, 10 m, 24 ene. 1995 (fr.), Aguilar 3733 (CR, USJ). [Cantón Osa], [Palmar], fachada sur de la Fila Retinto, filas y laderas del cañón de la Quebrada Benjamín, 08°59' N, 83°28'W, 300 m, 13 dic. 1989 (fr.), Hammel 17701 (CR); Palmar norte, [08°58'07.3"N, 83°27'58.6"W], [40 m], 05 feb. 1976, Poveda & Sáenz 1277 (CR); Palmar sur, 05 feb. 1976, Poveda & Sáenz 1077 (USJ). Cantón Parrita, El Carmen, 600 m, feb. 2000 (fr.), Nuñez 9 (JVR). **San José**. Cantón Montes de Oca, San Pedro, contiguo al Laboratorio de Tecnología Poscosecha, Ciudad de la Investigación, Universidad de Costa Rica, 9°56'24.5"N, 84°02'40.8"W, 1295 m, 12 dic. 2019 (fl., fr.), Aguilar-Sandí 17 (USJ) [cultivado]; Campus de la Universidad de Costa Rica, Jardín Botánico Orozco, [09°56'07.3"N, 84°03'05.7"W], 1200 m, 26 set. 2012 (fr.), Morales 2345 (USJ) [cultivado]. Cantón San José, Jardín del Museo Nacional de Costa Rica, 09°56'00"N, 84°04'30"W, 1100 m, 01 dic. 1994 (fl.), Cascante 406 (CR) [cultivado]. Cantón Santa Ana, Santa Ana, parqueo de la Plaza Koros, 09°55'58.6"N, 84°10'42.6"W, 900 m, 21 abr. 2019 (fr.), Aguilar-Sandí 13 (USJ) [cultivado]. **EL SALVADOR. La Libertad**. San Andrés, [457 m], 04 feb. 1959 (fl.), Allen 7216 (EAP). **San Salvador**. Finca Altamira, hills south of San Salvador, [853 m], 22 abr. 1958 (fr.), Allen & Almour 6856 (EAP). **San Vicente**. Vicinity of San Vicente, 400–500 m, 7–14 feb. 1947 (fr.), Standley & Padilla 3714 (EAP). **Sonsonate**. About 16 km east of headquarters of Hacienda Las Tablas, near Río Acachapa, 13°39'N, 89°34'W, 780 m, 08 may. 1942 (fl.), Tucker 1356 (EAP). **GUATEMALA. El Petén**. El Ceibo, 90 m, Ortiz 6552 (EAP). **HONDURAS. El Paraíso**. El Paraíso, Escuela de Río Arriba, ca. 2 km al sur de la ciudad de El Paraíso, cultivado, 20 jun. 1996 (fl.), Linares 3438 (EAP). **Francisco Morazán**. Tegucigalpa, esquina norte del Colegio San Francisco, 950 m, 24 feb. 1983 (fr.), Nelson & Sosa 8536 (TEFH). **MÉXICO.** [**Campeche**]. Calakmul, a 40 km al este de Dos Naciones, camino a El Civalito, 17°57'40"N, 89°20'28"W, 207 m, 30 jul. 1997 (fr.), Martínez 27895 (EAP). **Chiapas**. Escuintla, Cacaluta, 12 may. 1947 (fr.), Matuda 16529 (EAP).

Notas. Existen árboles cultivados en sitios urbanos del Valle Central (900–1200 m), con 15–38 m de altura y 80–106 cm de DAP. Se encuentran en: jardín del Museo Nacional de Costa Rica (*Cascante 406*, CR); parqueo de la Plaza Koros, Santa Ana (*Aguilar-Sandí 13*, USJ); terrenos del Centro de Conservación de Santa Ana, Santa Ana (Obs., pers.); campus de la Universidad de Costa Rica (*Morales 2345*, USJ; *Aguilar-Sandí 17*, USJ). Estos árboles no se incluyeron en el mapa de distribución, pero son una fuente accesible de germoplasma, aspecto a tener en cuenta en estudios de conservación.

La especie ha sido registrada en el Parque Nacional Carara a 638 m de altitud (Jiménez & Grayum 2002), pero no hay testigos de herbario de esta localidad. Por otra parte, Standley (1938) y Jiménez (1998) indicaron que esta especie está presente en Guanacaste, lo cual se respalda con dos recolectas (*Acosta 1111*, CR; *II INBio 150*, CR). Sin embargo, no está claro si son recolectas del mismo árbol o de árboles diferentes; tampoco se sabe si se trata de árboles en estado silvestre o cultivados.

Myroxylon balsamum es un árbol de 15–50 m de altura, con peridermis lenticelada, hojas imparipinnadas, alternas, folíolos alternos (raro subopuestos), lámina de los folíolos 4.5–8.5(–12.5) × 2–4.5 cm, con puntos y rayas translúcidos (poco evidentes en material fresco), ápices acuminados a largamente acuminados, inflorescencias racemosas, flores papilionáceas, cáliz lobulado, estandarte estrechamente ovado, frutos samaroides, cámara seminífera subglobosa (en frutos maduros), 1 o 2 semillas reniformes, testa lisa. Estas características contrastan con las de *M. peruiferum* (Cuadro 1).

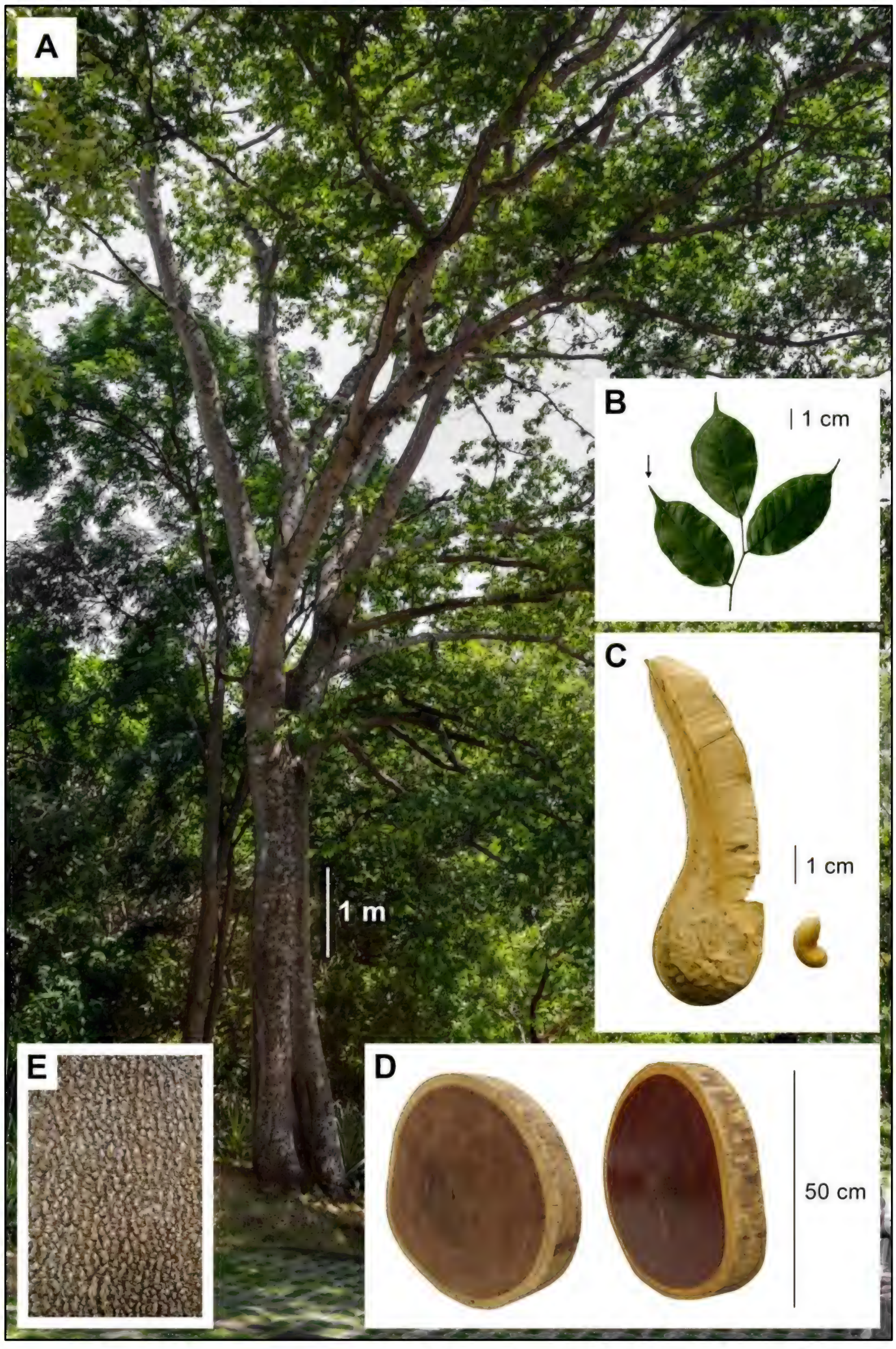

Figura 2. *Myroxylon balsamum* (Fabaceae). A. Tronco y copa. B. Detalle de los folíolos distales (la flecha señala el ápice). C. Fruto y semilla. D. Madera en corte transversal (izq. en bruto; der. pulida y barnizada). E. Detalle de la peridermis lenticelada. [A–C y E: *Aguilar-Sandí 13* (USJ); D: col.: *Poveda, Jiménez & Burger* s.d. (JVR); la muestra procede de Palmar Norte de Osa, Puntarenas]. Las fotografías son del autor.

Cuadro 1. Características morfológicas para diferenciar las especies del género *Myroxylon*

Característica	*M. balsamum*	*M. peruiferum*
Tamaño de los folíolos	4.5–8.5(–12.5) × 2–4.5 cm	3–4.5(–7.5) × 1.5–3 cm
Ápice de los folíolos	Acuminado a largamente acuminado	Retuso a acuminado
Lobulación del cáliz[a]	Lobulado	No lobulado
Forma del estandarte[b]	Estrechamente ovado	Ampliamente ovado
Cámara seminífera[c]	Subglobosa	Aplanada
Testa de la semilla	Lisa	Rugosa

[a, b] En Aguilar-Sandí (2019) pueden verse fotografías de las flores. [c] En frutos maduros.

MYROXYLON PERUIFERUM L.f., Suppl. Pl. 233. 1781 [1782]. *Myrospermum peruiferum* (L.f.) DC., Prodr. 2: 95. 1825. *Toluifera peruifera* (L.f.) Baill., Hist. Pl. 2: 383. 1870. **TIPO: America meridionalis**. s.d., *Mutis* s.n. (P00679272). Fig. 3.

Myrospermum pedicellatum Lam., Encycl. 4(1): 191. 1797. *Toluifera pedicellata* (Lam.) Baill., Hist. Pl. 2: 383. 1870. **LECTOTIPO** (Sartori et al. 2015): **Perú**. s.d., *Jussieu s.n.* (G00404303).

Myroxylon pubescens Kunth, Nov. Gen. Sp. 6: 374. 1823. *Myrospermum pubescens* (Kunth) DC., Prodr. 2: 95. 1825. *Toluifera pubescens* (Kunth) Baill., Hist. Pl. 2: 383. 1870. **LECTOTIPO** (Sartori et al. 2015): **America equatorial**. Cartagena, s.d., *Bonpland 1890* (P00151682).

Myrospermum erythroxylum Allemão, Rev. Braz. 1: 51. 1857. **LECTOTIPO** (Sartori et al. 2015): **Brazil**. Rio de Janeiro, s.d., *Allemão* s.n. (BM000053824).

Myroxylon robiniaefolium Klotzsch, Bonplandia 5(17): 276. 1857. **LECTOTIPO** (Sartori et al. 2015): **Ecuador**. s.d., *Warszewicz s.n.* (BM000053832; isolectotipo: K500797).

Distribución. Cuenca del río Barranca, 900–1200 m, provincia de Alajuela, cantones de San Ramón y San Mateo. Estribaciones montañosas al suroeste del Valle Central, 900–1300 m, provincia de San José, cantones de Acosta, Mora y Santa Ana. Estos sitios están ubicados en las regiones climáticas Central y Pacífico Central, presentan estacionalidad climática marcada (estación seca de diciembre a abril y lluviosa de mayo a noviembre), precipitación anual promedio de 2500 mm y temperatura media de 24 °C (Meza & Bonilla 1990; Aguilar-Sandí 2019).

Fenología. Especie perennifolia. Floración de febrero a abril; fructificación de abril a octubre.

Nombres comunes. Chirraco, chirraca.

Usos. Chirraca y chirraco son términos empleados únicamente en Costa Rica; siendo chirraca el nombre de la resina producida por los chirracos, es decir, por los árboles (Gagini 1919; Diccionario Enciclopédico Quillet 1974). A pesar de ello, no hay registros oficiales del uso de esta resina en el país. La madera es extremadamente pesada (peso específico aprox. 0.95 g/cm^3), aromática y resistente a la pudrición (Lorenzi 2002). En Costa Rica ha sido explotada de la misma forma que la madera de *M. balsamum* (F. Rodríguez, com. pers., 2019). Se conoce su uso en la confección de ejes, ruedas y timones de carreta (F. Zamora, com. pers., 2020).

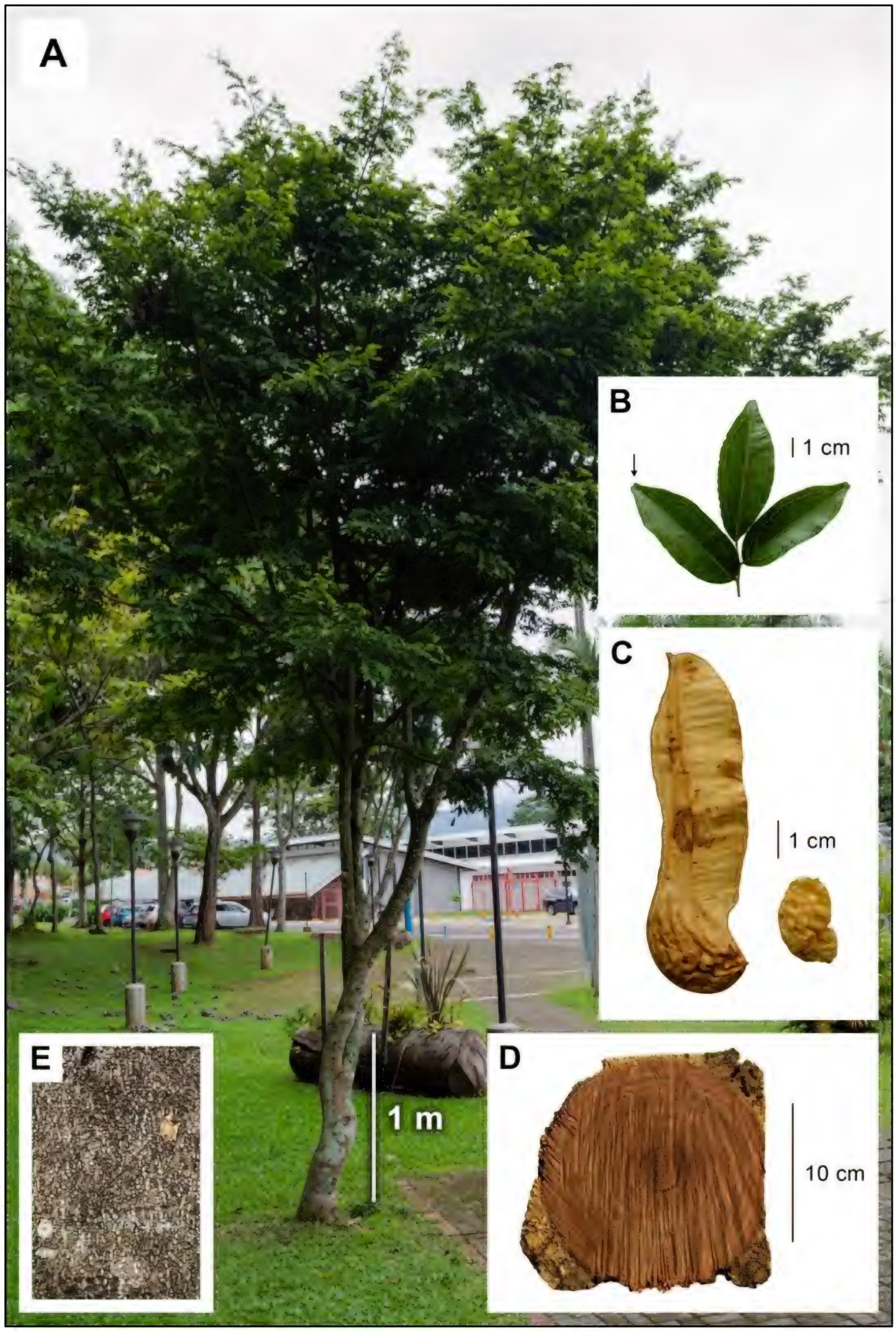

Figura 3. *Myroxylon peruiferum* (Fabaceae). A. Tronco y copa. B. Detalle de los folíolos distales (la flecha señala el ápice). C. Fruto y semilla. D. Madera en corte transversal (sin pulir). E. Detalle de la peridermis lenticelada. [A–B y E: árbol ubicado en el campus de la Universidad de Costa Rica, Montes de Oca, San José; C: *Aguilar-Sandí 10* (USJ); D; de un árbol caído naturalmente en el sitio de recolecta de *Aguilar-Sandí 16* (USJ)]. Las fotografías son del autor.

Estado de conservación. Desconocido en Costa Rica. Especie clasificada como no amenazada en Catalogue of Life (2019) y no incluida en la Lista Roja (UICN 2019).

Ejemplares examinados seleccionados. COSTA RICA. Alajuela. [Cantón Alajuela], [Parque Central de Alajuela], [10°00'59.1"N, 84°12'50.3"W], jul. 1958 (fr.), *Jiménez* s.n. (CR 36550, USJ 6507) [cultivado]. Cantón San Mateo, mar. 1918, *Jiménez 1218* (CR). Cantón San Ramón, San Rafael, Rincón de Mora, 10°02'41.6"N, 84°28'22.4"W, 1200 m, 23 nov. 2019, *Aguilar-Sandí 16* (USJ); Piedades Sur, San Francisco, [cuenca del río Barranca], 10°04'40.3"N, 84°32'27.6"W, 900 m, 18 ene. 2020, *Aguilar-Sandí 18* (USJ). **San José**. Cantón Acosta, San Ignacio, parque central, 09°47'55.3"N, 84°09'46.0"W, 1097 m, 20 abr. 2019 (fr.), *Aguilar-Sandí 10* (USJ); San Ignacio, poblado de Chirraca, Viña El Espavey, 09°48'41.4"N, 84°10'38.0"W, 980 m, 20 abr. 2019 (fr.), *Aguilar-Sandí 11* (USJ). Cantón Montes de Oca, Sabanilla, campus UCR, entrada a UCAGRO, 09°56'22.4"N, 84°02'53.1"W, 1200 m, 19 feb. 2019 (fl.), *Aguilar-Sandí 6* (USJ) [cultivado]; [San Pedro], Universidad de Costa Rica, [9°56'04.1"N, 84°03'08.5"W], [1200 m], 5 dic. 1973, *Poveda 795* (CR, JVR, USJ) [cultivado]. Cantón Mora, [Ciudad Colón], Hacienda El Rodeo, 09°54'59.5"N, 84°15'54.4"W, 900 m, 13 abr. 2019, *Aguilar-Sandí 9* (USJ); Zona Protectora El Rodeo, Reserva de la Universidad para la Paz, 09°54'20"N, 84°16'30"W, 850–900 m, 27 may. 1997, *Cascante 1324* (CR); El Rodeo, Valle del Tárcoles, Bajo Morales, 09°55'00"N, 84°16'00"W, 800–1000 m, 8 jul. 1995, *Jiménez 1889* (CR). Cantón Santa Ana, Salitral, Chirracal, 09°54'40.6"N, 84°10'25.5"W, 1225 m, 11 abr. 2019, *Aguilar-Sandí 7* (USJ); Chirracal, 09°54'44.1"N, 84°10'23.6"W, 1229 m, 11 abr. 2019, *Aguilar-Sandí 8* (USJ); Alto Raicero-Chirracal, 09°54'22.6"N, 84°10'11.0"W, 1220 m, 21 abr. 2019, *Aguilar-Sandí 12* (USJ). **EL SALVADOR. Ahuachapán**. Vicitiny of Ahuachapán, 700–1100 m, 16–25 ene. 1947 (fl., fr.), *Standley & Padilla 2899* (EAP) [identificado como *M. balsamum*]. **NICARAGUA. Chontales**. Along road between Río Bizcocho and Río El Jordán, near confluence with Río La Pradera, [12°12'00.0"N, 85°15'00.0"W], 350–550 m, 18 feb. 1984 (fl.), *Stevens 22871* (TEFH) [identificado como *M. balsamum*].

Notas. Existen árboles cultivados en el campus de la Universidad de Costa Rica, Montes de Oca (*Poveda 795*, CR, JVR, USJ; *Aguilar-Sandí 6*, USJ) y en el Parque Central de Alajuela (*Jiménez* s.n., CR 36550, USJ 6507). Estos árboles son una fuente accesible de germoplasma. Debido a que son cultivados, no se incluyeron en el mapa de distribución.

En esta sinopsis se incluyen recolectas de *M. peruiferum* realizadas en la cuenca del río Barranca en San Ramón de Alajuela (*Aguilar-Sandí 16*, USJ; *Aguilar-Sandí 18*, USJ), localidad no considerada en Aguilar-Sandí (2019). En 1918, Otón Jiménez hizo una recolecta de *M. peruiferum* en San Mateo de Alajuela (*Jiménez 1218*, CR), pero el ejemplar se identificó correctamente hasta el año 2019.

Myroxylon peruiferum es un árbol de 15–30 m de altura, con peridermis lenticelada, hojas imparipinnadas, alternas, folíolos alternos, láminas de los folíolos 3–4.5(–7.5) × 1.5–3 cm, puntos y rayas translúcidos evidentes, ápices retusos a acuminados, inflorescencias racemosas, flores papilionáceas, cáliz sin lóbulos definidos, estandarte ampliamente ovado, frutos samaroides, cámara seminífera aplanada (en frutos maduros), 1 o 2 semillas reniformes, testa rugosa e impregnada de resina. Estas características contrastan con las de *M. balsamum* (Cuadro 1).

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NEW COMBINATION IN *CYMOPTERUS GLOMERATUS* (APIACEAE)

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ABSTRACT

Cymopterus acaulis var. *higginsii* (Welsh) Goodrich is endemic to Kane Co., Utah. These plants have a different petal and anther color combination and are allopatric with other infraspecific taxa within *Cymopterus glomeratus*. The taxon is recognized here as **Cymopterus glomeratus** var. **higginsii** (Welsh) K.M. Mason, **comb. nov.**

Sun et al. (2005) have recommended that *Cymopterus glomeratus* be treated as a highly variable species, with no varieties or subspecies. Other recent students of the group, however, have recognized infraspecific taxa (Hartman 2006; George et al. 2014; Goodrich 2015; Mansfield et al. 2017).

Plants that have been identified as *Cymopterus higginsii* Welsh are part of the *C. glomeratus* complex (Sun et al. 2005). Goodrich (2015) found it useful to continue to recognize *C. higginsii* at specific rank because it has a limited distribution, is allopatric from other taxa, and has a distinctively different combination of petal and anther colors. Mansfield et al. (2017) explicitly declined to recognize var. *higginsii*, following Cronquist (1997), who equated var. *higginsii* with var. *fendleri*. Var. *higginsii* is a dark purple-flowered form known only from Kane Co., Utah — its range is entirely surrounded by that of mostly yellow-flowered var. *fendleri*, and it is similar to that variety except in flower color, though there may also be subtle differences in habitat. These plants are justifiably recognized at varietal rank, consistent with other currently recognized intraspecfic taxa of *C. glomeratus*.

Cymopterus glomeratus var. **higginsii** (S.L. Welsh) K.M. Mason, **comb. nov.** *Cymopterus higginsii* S.L. Welsh, Great Basin Naturalist 35: 377. 1976. *Cymopterus acaulis* Raf. var. *higginsii* (S.L. Welsh) Goodrich, Great Basin Naturalist 46: 79. 1986. Higgins' spring-parsley

Key to varieties of *Cymopterus glomeratus*

1. Mericarp abaxial wings 0--0.2 mm high; carpophore present, deciduous; Colorado (Delta, Montrose, and Ouray cos.) ..... var. **concinnus**
1. Mericarp abaxial wings 0.4--3 mm high; carpophore absent; w USA, including Colorado (Delta, Montrose, and Ouray cos.).
2. Petals and anthers rose to purple; Utah (Kane Co.) ..... var. **higginsii**
2. Petals and anthers white or yellow, or if anthers purple then petals white or yellow; w North America, including Utah (Kane Co.).
3. Petals and anthers white (both yellow and white in the Uintah Basin of Utah) ..... var. **glomeratus**
3. Petals yellow, turning white or cream in age, rarely purple, anthers yellow.
4. Mericarp wings 2.5--3 mm high, planar or slightly wavy; sw Idaho, se Oregon ..... var. **greeleyorum**
4. Mericarp wings 0.4--2.5 mm high, wavy to strongly corrugated; Arizona, Colorado, New Mexico, Texas, Utah.

5. Peduncles 2--27 cm, usually equaling or exceeding leaves; mericarps 4--10 mm wide; plants 2--25 cm ; Arizona, Colorado, New Mexico, Texas, c and e Utah ..... var. **fendleri**
5. Peduncles 2.5--5.5 cm, usually shorter than, sometimes exceeding, leaves; mericarps 4--5 mm wide; plants 5--7(--8.5) cm; Utah (Millard and Tooele cos.) ..... var. **parvus**

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EULOPHIA GRAMINEA (ORCHIDACEAE) NATURALIZED IN TEXAS

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ABSTRACT

Eulophia graminea is reported here, based on photographic evidence, as naturally occurring in an urban landscape in Houston, Texas. It is the first report of the species from Texas and only the second from the USA.

Eulophia graminea (Orchidaceae) is a terrestrial orchid native to Asia discovered growing in mulched landscapes in Miami-Dade Co., Florida (Pemberton at al. 2008), its first known occurrence in the USA. It now has spread to a number of Florida counties (Kartez 2020; USDA, NRCS 2020). This orchid has a known natural distribution from Sri Lanka and India to China, the Ryuku Islands in Japan, and throughout most of southeast Asia, including Singapore (Keng et al. 1998). It is considered naturalized and weedy in Australia (Macrae 2020). Habitats of the species include maritime hammocks, e.g. coastal beaches, grasslands, roadsides, and other open areas at lower elevations (Ang et al. 2011).

The orchid was recently discovered in Texas in an urban landscape in northwest Houston, Harris County, Texas, documented here by photos taken of the naturalized population. Arrangements are being made for collection of a voucher (to be placed at BAYLU) during the next flowering period.

Texas. Harris Co.: Northwest Houston, NW corner of Beltway 8 (Sam Houston Parkway/Tollway) and Hwy 249, 2 mi SE of Willowbrook, ca. 2 mi ESE of Sam Houston Race Park, 9 Aug 2020, photos by Kelly Sennhauser. Figs. 1-3.

Eulophia graminea was found in Texas in June 2019 as scatted individuals and in clusters in an urban/garden woodlot in openings between native loblolly pine and water oak and introduced urban landscape plantings. The orchid grows in leaf litter and pine straw and among colonies of *Carex cherokeensis*. Other associated species include *Calyptocarpus vialis*, *Celtis laevigata*, *Commelina erecta*, *Crinum americanum*, *Cyperus* sp., *Diodia virginiana*, *Euphorbia cyathophora*, *Ilex vomitoria*, *Solidago sp.*, and *Stenotaphrum secundatum*.

Flowering was over in June and the plants had produced capsules. Mature individuals have large pseudobulbs (Fig. 2) and in August, one pseudobulb of those observed in June produced flowers (Figs. 1, 3). The landowner, a member of the Houston Orchid Society, recognized the plant as an orchid and photos were sent to the authors, who determined the species to be *Eulophia graminea.*

During February 2020, what appears to be initiation of flower stalks (bolting) from one of the pseudobulbs indicates that the orchid is initiating flowering, which should occur in summer 2020.

Figure 1. *Eulophia graminea*, Harris Co., Texas. Photo by Kelly Sennhauser, 9 August 2020 (used with permission).

Figure 2. Pseudobulb of *Eulophia graminea*, Harris Co., Texas. Photo by Kelly Sennhauser, 9 August 2020 (used with permission).

Figure 3. Flower of *Eulophia graminea*, Harris Co., Texas. Photo by Kelly Sennhauser, 9 August 2020 (used with permission).

A brief description and color photos of *Eulophia graminea* are provided by the North American Orchid Conservation Center (2020). This species is self-compatible and considered to have potential to spread by airborne seeds and by pseudobulbs transported in mulch, soil, and in plantings of other orchids (Pemberton et al. 2008). In Florida "*Eulophia graminea* forms a dense monoculture and is now found in rockland hammock and pine rockland habitats and cypress strands, growing in rock, sand, mulch, and bare earth. [It has] potential to become an invasive plant. ... Its native range has colder temperatures than Florida, suggesting it may spread northward" (North American Orchid Conservation Center 2020).

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STATUS AND FIRST RECORD OF *CASTILLEJA PARVIFLORA* (OROBANCHACEAE) FOR CALIFORNIA

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ABSTRACT

A recent collection of *Castilleja parviflora* Bong. from Plumas Co., California, is documented and illustrated. This collection represents both a southward range extension and a first verified occurrence for this species in the state of California. Previous usages of the name *Castilleja parviflora* in California botanical literature are discussed and assigned to other species.

Castilleja parviflora Bong. is a wide-ranging and variable species primarily restricted to the states and provinces of the greater Pacific Northwest region. The species was originally described from the vicinity of Sitka, Alaska (Bongard 1833), and four regional varieties are presently accepted (Egger et al. 2019). The southernmost of these is var. *oreopola* (Greenm.) Ownbey, which is found from the Mt. Rainier region in Lewis and Pierce counties, Washington, southward in the Cascade Range to the Three Sisters region of central Oregon in Deschutes and Lane counties. Effective lectotypification of the basionym *Castilleja oreopola* Greenm. was published by Marion Ownbey (1959) (Fig. 1). Plants of var. *oreopola* have distally colorful bracts, usually ranging from pink to pink-purple or magenta, with occasional variants of crimson, white, or other shades, and they often form conspicuous displays in moist to fairly dry subalpine meadows (Fig. 2).

The name *Castilleja parviflora* has been included at times in the past as part of the flora of California, but these historical applications do not correspond to our present understanding of the species and are referable to other species. The name has been misapplied to variations of the widespread Californian species *C. affinis* Hook. & Arn., in the form of *C. parviflora* var. *californica* (Abrams) Zeile (1925) and *C. parviflora* var. *douglasii* (Benth.) Jeps. (1901), both of which are now regarded as synonyms of the typical form of *C. affinis*. More recently, the *Castilleja* treatment in the first edition of the Jepson Manual (Chuang & Heckard 1993) included *C. parviflora* as a repository for *C. peirsonii* Eastw., which was reduced to synonymy under *C. parviflora* in that volume. However, that synonymy has since been rejected both in the second edition of the Jepson Manual (Wetherwax et al. 2012), as well as in the recent Flora of North America (Egger et al. 2019), and *C. peirsonii* is now accepted as a full species related to but not synonymous with *C. parviflora*.

On 23 June 2015, Jim Battagin, Dana Flett, and Dana Ludington visited Aster Fen, a small wetland in the Plumas National Forest, for botanical survey work. They located an unknown *Castilleja* species with pink-purple bracts growing in the vicinity of the fen and photographed some of the plants. Subsequent efforts to match the plants with known *Castilleja* species of the region

proved unsuccessful. Battagin subsequently sent photos of the plants to Egger, who confirmed they did not match any vouchered species from California. On 28 July 2019, the three botanists and others revisited Aster Fen and obtained a few flowering specimens and additional photographs (Figs. 5-9), as well as tissue for genetic analysis. Egger was later able to verify the specimens as the first vouchered collection of true *C. parviflora* for California and to further confirm them as reasonably typical var. *oreopola*. This collection also represents a southward disjunction of about 550 kilometers for *C. parviflora* var. *oreopola*.

California. Plumas Co.: Sierra Nevada, Plumas National Forest, Bucks Lake Wilderness Area, Aster Fen, 39.95047, -121.15976, 6721 ft (2323 m), 28 Jul 2019, *Battagin et al. s.n.* (WTU). (Figs. 3-4).

Aster Fen is 1.2 acres in extent and consists of a very wet, well-developed, non-serpentine peat substrate over granitic bedrock. The fen is bordered by a band of *Alnus incana* subsp. *tenuifolia*, in turn surrounded by a mixed conifer forest mostly consisting of *Abies magnifica* and *Pinus contorta*. The *Castilleja* plants occur largely around the margins of the fen, though some plants occur throughout, except for the portions with standing water. Other plant species found in Aster Fen include *Sphagnum subsecundum*, *Philonotus fontana*, *Polygonum bistortoides*, *Drosera rotundifolia*, *Kalmia polifolia*, *Parnassia palustris*, *Vaccinium uliginosum* var. *occidentale*, *Viola macloskeyi*, *Primula tetrandra*, *Pedicularis attolens*, *Erythranthe primuloides*, *Hypericum anagalloides*, and *Oreostemma alpigenum* var. *andersonii*. *Agrostis humulis*, *Muhlenbergia filiformis*, *Carex echinate*, *Carex limosa*, *Carex luzulina*, *Carex simulata*, *Carex utriculata*, *Eleocharis quenqueflora*, *Spiranthes romanzoffiana*, *Tofieldia glutinosa*. Many of the *Castilleja* plants were associated with and possibly parasitic on the *Kalmia* or *Vaccinium* species.

The southward disjunction of this species could be attributed to dispersal by migratory birds, a mechanism hypothesized for other *Castilleja* species (Tank & Olmstead 2009). Alternatively, the Aster Fen population may be relictual from an earlier, likely recent Pleistocene cold period and maintained there by the cooling effects of the relative high elevation and mesic nature of the habitat.

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Figure 1. Lectotype (GH) of *Castilleja parviflora* var. *oreopola* from Mt. Adams, Yakima Co., Washington. The name "var. alpina" as applied here (not T.C. Porter 1874) is a later homonym.

Figure 2. *Castilleja parviflora* var. *oreopola*, Burroughs Mountain Trail, Mt. Rainier National Park, Pierce Co., Washington, 23 Jul 2009. Photo by Mark Egger.

Figure 3. *Castilleja parviflora* var. *oreopola*, Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019, *Battagin et al. s.n.* (WTU).

Figure 4. *Castilleja parviflora* var. *oreopola*, Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019, *Battagin et al. s.n.* (WTU).

Figure 5. *Castilleja parviflora* var. *oreopola*, Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019. Photo by Jim Battagin.

Figure 6. *Castilleja parviflora* var. *oreopola*, Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019. Photo by Jim Battagin.

Figure 7. *Castilleja parviflora* var. *oreopola*, Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019. Photo by Jim Battagin.

Figure 8. *Castilleja parviflora* var. *oreopola*, Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019. Photo by Jim Battagin.

Figure 9. A portion of Aster Fen, Bucks Lake Wilderness Area, Plumas Co., California, 28 Jul 2019. Photo by Jim Battagin.

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TAXONOMIC DECISIONS AT GENERIC RANK IN TRIBE ASTEREAE (ASTERACEAE) FOR THE GLOBAL COMPOSITAE DATABASE

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ABSTRACT

The account of Astereae for the Global Compositae Database (GCD) includes 208 genera. Most of the decisions regarding which to recognize are straightforward but some are relatively subjective and will not meet with unanimous agreement. Five genera of Conyzinae are recognized that are nested within the phylogenetic branches of *Erigeron*. *Oligoneuron* apparently is sister to *Solidago* sensu stricto and is treated as a distinct genus (**Oligoneuron vossii** (Pringle & Laureto) Nesom, **comb. nov.**, completes the nomenclature) but as sisters they might be regarded as congeneric. Most of the generic segregates of Old World *Aster* are retained in the GCD account although most of them are within the cladistic bounds of *Aster* sensu stricto as recently proposed — *Aster* as so proposed, however, is highly diverse and it seems probable that narrower concepts of genera will eventually be accepted. Taxonomic decisions regarding several other examples of North American genera also are discussed, particularly where morphology and geography do not accord with taxonomy based on molecular phylogeny.

The Global Compositae Database (GCD; Compositae Working Group 2020) aims toward providing an account of the genera and species of the entire family and their taxonomic arrangement. The Astereae contribution so far has been limited to modifications and additions of currently recognized genera of Astereae, leaving the editing and arrangement of species (especially in larger genera) as a second step — both steps involve consideration of morphological, molecular, and geographic evidence. The current (10 April 2019) GCD account recognizes 208 genera of Astereae.

Most of the decisions are relatively straightforward but some do not find complete agreement among taxonomists. Those controversial perhaps to a greater degree are illustrated here by examples in *Erigeron*, Old World *Aster*, and a few other genera. For *Erigeron* and *Aster*, molecular data have accumulated toward an understanding of species relationships. In *Erigeron* (about 400 species, with a North American center of diversity), a relatively complete overview is at hand. A relatively consistent view of the overall phylogenetic structure of Old World *Aster* (200+ species) also is emerging.

In *Erigeron*, decisions regarding generic rank rest on whether or not to recognize morphologically distinct taxa whose evolutionary origin is within the branches of the genus and whose separation leaves the genus non-monophyletic. For many, consistent objectivity and the goal of recognizing only monophyletic genera simplify such decisions. Toward a pragmatic taxonomy (with distinctive genera of consistent morphology), however, a few of these taxa are recognized at generic rank in the GCD, with the acknowledgment that their evolutionary position is clear and understood.

Taxonomic decisions in the Old World *Aster* "complex" are in part related to the lack of a detailed morphological overview of the entire group and commitments to a formally revised taxonomy. Numerous genera remain to be described. Examples are provided from other North American groups where molecular data underlie decisions that appear to be contradicted by morphological and geographic evidence.

The primary problems involved here are not new, nor are the taxonomic alternatives. The aim of this brief commentary is to put the basis of these GCD decisions in Astereae on record, pointing out

common kinds of problems that may exist unnoticed within what might seem to be a uncomplicated account.

Erigeron

Species identified as *Conyza* have arisen independently within *Erigeron* at least two times, and the diagnostic feature of *Conyza*, short-ligulate ray flowers, appears elsewhere sporadically throughout *Erigeron*. The type, *Conyza chilensis* (= *Erigeron primulifolia*), is in the same clade as the cosmopolitan *Erigeron* [*Conyza*] *bonariensis* and various *Erigeron* species of Mexico and South America. The majority of the ca. 60-100 South American *Conyza* species also appear to share this relationship but have not been analyzed molecularly. The world-wide weed *Erigeron* [*Conyza*] *canadensis* is in a different clade with *Erigeron* [*Conyza*] *apurensis*, *E. leptorhizon*, the Revillagigedo Islands endemics *E. crenatus* and *E. socorroensis*, and *E. divaricatus* (= *Conyza ramosissima*). Conyzas were treated within *Erigeron* until the 1940's and names as *Erigeron* for most species are in place — all of these species are treated as *Erigeron* in the GCD.

Aphanostephus, including 4 species (plus varietal taxa) of the south-central USA and northern Mexico (Nesom 2006, 2008), had never been suspected of a close relationship with *Erigeron* until molecular data (Noyes 2000; Andrus et al. 2008) indicated that it shares immediate ancestry with a group of Caribbean *Erigeron*, a group of Mexican species, and *Darwiniothamnus*. In its involucral morphology and achene morphology (wall structure, surface vestiture, and pappus) there is nothing comparable in *Erigeron*, and its chromosome number of x=5 contrasts with the otherwise invariable x=9 within the cladistic branches of *Erigeron* sensu lato (subtr. Conyzinae). Even with the understanding that *Erigeron* thus is non-monophyletic, *Aphanostephus* was included at generic rank in the Flora of North America (Nesom 2006) and it also is treated as such in the GCD.

Darwiniothamnus sensu stricto (*Erigeron tenuifolius* and *E. lancifolius* of the Galapagos Islands) was segregated from *Erigeron* in 1962 on the basis of its shrubby, "rosette" habit, leaves in terminal whorls with short internodes, heads in a condensed corymbiform capitulescence, and slightly dimorphic ray and disc achenes. Molecular data (Andrus et al. 2008) indicate that these sister species are most closely related to Mexican and Caribbean species of *Erigeron*, and the distinctive growth form of *Darwiniothamnus* developed in parallel with other Asteraceae species of oceanic islands. In the GCD, *Darwiniothamnus* is placed within *Erigeron*, although there is justification for its separation as a genus.

Evolutionary divergence within the branches of *Erigeron* sensu lato among species with an "austro-brasilien" distribution has been pronounced. Four distinctive species groups from this region, comprising a single clade, are treated in the GCD at generic rank — this clade is closely related to *Erigeron primulifolia*, *Erigeron bonariensis* and probably most of the South American conyzas, South American species traditionally identified as *Erigeron*, and two primarily Mexican species groups. Species of the sisters ***Neja*** (6 species) and ***Hysterionica*** (7 species) are consistently yellow-rayed (yellow otherwise rare in *Erigeron*) and the numerous, raised, resinous-glandular achenial ribs of *Neja* are unique within *Erigeron* sensu lato. Prior to their segregation at generic rank, the two species of ***Apopyros*** were identified as *Aster* — they are characterized by shiny-indurate, parallel-veined, strictly cauline leaves, disciform heads with eligulate ray flowers, and subterete, 5-nerved achenes. The plants are fire-adapted, the tall, erect stems arising quickly after a burn from a thick, woody rhizome or tuber. ***Leptostelma*** (6 species), with prominent white or yellow rays and compressed achenes, is the most *Erigeron*-like of these four genera. Bentham (Genera Plantarum, 1873) and Baker (Flora Brasiliensis, 1882) treated the two original species as *Erigeron* sect. *Leptostelma* and Cabrera described four of the species in 1957 and 1959, placing them in *Erigeron*. Teles et al. (2008) completed the nomenclature in *Leptostelma*. *Leptostelma* is disjunct from the range of typical South American *Erigeron*, which is centered in the Andean region, but sympatric with species of conyzoid species. For consistency within this remarkable clade, it is recognized at generic rank.

Old World Aster complex

The overall evolutionary structure of Old World aster is becoming relatively clear in molecular analyses (Li et al. 2012; Jafari et al. 2015; Korolyuk et al. 2015). The main groups and many critical species have been included, although perhaps less than half of the species have been sampled. No formal, matching taxonomic framework exists but an excellent informal overview is provided by Li et al. (2012). Main features of the recent molecular-phylogenetic arrangements are noted below.

* *Galatella*, *Tripolium*, and *Crinitina* (the *Galatella* clade) are sister to the Bellidinae. Li et al. (2012) have suggested that all three may be appropriately treated as a single genus; Jafari et al. (2015) suggest that *Tripolium* and *Galatella* are distinct. Based on morphology, Karanović et al. (2015) also found that each of the two is distinct.

* *Chamaegeron* and *Lachnophyllum* together are sister to the *Galatella*-Bellidinae clade.

* *Sheareria* is placed as sister to the *Kalimeris* clade by the analyses of Li et al. (2012) and Korolyuk et al. (2015) but by Li et al. (2017) as sister to the *Aster amellus* clade.

* The *Kalimeris* clade (the *Aster ageratoides* group) includes species of *Kalimeris*, *Heteropappus*, *Aster ageratoides*, *A. orephilus*, *A. souliei*, and others. *Kalimeris* and *Heteropappus* are not each other's closest relative within the larger clade.

* The morphologically diverse *Aster amellus* clade (*Aster* sensu stricto) includes *Rhinactinidia*, *Rhychospermum*, *Miyamayomena*, *Turczaninowia*, *Aster tataricus*, *Aster baccharoides*, *Aster maackii*, *Aster alpinus*, and others. *Miyamayomena angustifolia* (= *Aster sinoangustifolius*) is sister to the *Kalimeris-Aster amellus* clade pair.

* The "doellingerioid" species (*Aster scaber* et al.) are sister to the *Asterothamnus* clade, which includes *Asterothamnus*, *Arctogeron*, *Aster sikuensis*, *A. falcifolius*, and others. Species of *Kemulariella* (see Firat 2016) have not been sampled, but it seems likely from their Caucasus geography that they belong in the *Asterothamnus* clade.

* *Aster hersileoides* and *A. nitidus* as a pair are basal to the large *Aster* sensu stricto of Li et al. (2012), which includes the *Kalimeris*, *Aster amellus*, and *Asterothamnus* clades.

* *Psychrogeton* (excluding *P. obovatus*) and *Neobrachyactis* also are basal to the large *Aster* sensu stricto of Li et al.

* *Callistephus*, the morphologically isolated *Aster longipetiolatus*, *Myriactis Neobrachyactis*, and *Psychrogeton* are in a clade along with several apparently natural groups of *Aster* (e.g., *A. diplostephioides*, *A. asteroides*, *A. flaccidus*, *A. panduratus*, *A. fuscescens*, and others. The *Callistephus* group is either sister to all other Old World aster species or in an unresolved position related to the Australasian lineage.

Li et al. (2012) have suggested that *Aster* sensu stricto follow the boundaries of the molecular analysis to include the *Kalimeris*, *Asterothamnus*, and *Aster amellus* clades, with recognition of distinctive inner groups at the rank of section and series (e.g., *Arctogeron*, *Asterothamnus*, *Kemulariella*, *Psychrogeton*, *Rhinactinidia*, *Rhynchospermum*, and *Sheareria*, plus other previously unnamed species groups). They point out 18 species in 8 groups that should be removed from *Aster* and treated at generic rank.

Li et al. (2012) noted that their recircumscribed *Aster* sensu stricto remains morphologically complex — it seems probable that future taxonomy will argue for morphologically more homogeneous genera, with recognition of some smaller groups and isolated species within *Aster* (sensu Li et al.) at generic rank. For the GCD, pending a generally accepted taxonomy that accounts for new insights (via DNA and morphology) into phylogenetic structure and provides accompanying morphological definitions, all of these formally named segregates are recognized at generic rank with an implicit understanding of their phylogenetic position.

Symphyotrichum

The mostly North American *Symphyotrichum* (ca. 100 species) includes distinctive and mostly non-intergrading species groups. Among them, sect. *Conyzopsis* (3 species; the genus *Brachyactis*) is arguably the most distinctive — the plants are taprooted annuals with a unique chromosome number of *x*=7, biseriate and accrescent pappus, and ray florets in an outer zone of 2-4 series, with ligules absent or greatly reduced. While molecular data clearly indicate that *Brachyactis* arose from within x=8 *Symphyotrichum* (e.g., Vaezi & Brouillet 2009), this small group is morphologically and cytologically isolated from the rest of the genus and the rationale for not treating it at generic rank rests on a requirement for strictly monophyletic genera. Since the recent realignment of genera within American asters (in 1994), it has generally been included and accepted within *Symphyotrichum*.

Doellingeria-Eucephalus

Doellingeria (3 species, eastern North America) and *Eucephalus* (10 species, northwestern North America) are evolutionarily sister genera (e.g., Brouillet et al. 2009). They are morphologically distinct, particularly in involucres, fruits, ray color, and habit (*Eucephalus* is rhizomatous, *Doellingeria* fibrous-rooted), and there has never been a question about their delimitation. Based on plastid and ITS/ETS DNA data, however, Allen et al. (2019) have shown that *E. elegans* is sister to the *Doellingeria* species rather than to the rest of *Eucephalus*. They hypothesize that genetic interchange occurred in a hybridization event during early radiation of the *Doellingeria-Eucephalus* clade. In order to make the molecular-phylogenetic topology and the nomenclature congruent, they have enlarged *Doellingeria* to 13 species by formally transferring the *Eucephalus* species into it.

A genetic influence of *Doellingeria* on *Eucephalus elegans* is evident neither in morphology nor geography — the species of *Eucephalus* differ among themselves in relatively small ways and *E. elegans* is in no way out of place. *Doellingeria* and *Eucephalus* are discontinuously distinct and are maintained as such in the GCD. The paleo-historic and vestigial effect of hybridization can be pointed out by reference to a cladogram derived from molecular data.

Solidago and Oligoneuron

Oligoneuron (7 species) is treated by Semple and Cook (2006) as congeneric with typical *Solidago* (ca. 120 species) but the two are morphologically discontinuous and easily distinguished. Species nomenclature for *Oligoneuron* is completed below with a new combination. The horticultural entity x*Solidaster* was formed spontaneously in Europe as a garden hybrid between *Oligoneuron album* (*Aster ptarmicoides* = *Solidago asteroides*) and *Solidago canadensis* (Schilling et al. 2008) but natural hybrids are not known (comments in Nesom 1993). Although it clearly is closely related to *Solidago*, molecular data have not resolved the phyletic position of *Oligoneuron* (e.g., Semple et al. 1999; Brouillet et al. 2009) — an intuitive diagram shown by Semple (2016) indicates a sister relationship with *Solidago*. *Oligoneuron* is placed as a separate genus in the GCD.

Oligoneuron vossii (Pringle & Laureto) Nesom, **comb. nov.** *Solidago vossii* Pringle & Laureto, Michigan Bot. 49: 108. 2010.

An octoploid, apparently with ancestry involving *Oligoneuron houghtonii* and *O. album*, known only from Crawford and Kalkaska counties, Michigan (Laureto & Pringle 2010; Michigan Flora Online 2020).

Toiyabea

Based on morphological and geographic evidence, the genus *Toiyabea* has been expanded from one species to include three other species previously placed in *Tonestus* and *Lorandersonia* (both of the latter genera are still recognized) (Nesom 2020). Distribution of the four *Toiyabea* species in the previous taxonomy suggests that interpretations were over-reliant on ambiguous molecular data and/or that ancestral hybridization influences the structure of phylogenetic trees but has little or no influence on extant morphology and current geography.

Mexican species in the Gundlachia-Gutierrezia group

The genus *Aquilula* was established (Nesom 2018) to accommodate a highland Mexican species that, along with three other species of desert habitats of Mexico, was placed by Urbatsch and Roberts (2004) in the Caribbean genus *Gundlachia*. The Mexican species are morphologically and geographically disparate when joined to the Caribbean clade and molecular data do not contradict keeping them separate (as *Gundlachia* with 7 species, monotypic *Aquilula*, and *Xylothamia* sensu stricto with 3 species).

Medranoa (1 species), *Chihuahuana* (1 species), *Xylovirgata* (1 species), and *Neonesomia* (2 species) were described as new genera of the Chihuahuan Desert by Urbatsch and Roberts (2004), segregated from a clearly polyphyletic *Xylothamia*. Despite strong morphological distinctions among the species, molecular data indicate that they are closely related and the data do not provide unambiguous support for recognition of four closely related new genera among five species. Close geographic proximity and the production of zygomorphic disc corollas by each support their recognition as a single lineage. All five species have been united within *Medranoa* (Nesom 2007), with *Chihuahuana*, *Neonesomia*, and *Xylovirgata* treated as synonyms.

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UNA NUEVA ESPECIE DE *CRITONIA* (COMPOSITAE-EUPATORIEAE) DE LA SIERRA MADRE DEL SUR DE GUERRERO, MÉXICO

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RESUMEN

Se describe como nueva y se ilustra a **Critonia guerrerensis** Rzed., **sp. nov.**, a partir de material colectado en la parte alta de la Sierra Madre del Sur de Guerrero. El taxón nuevo pertenece al grupo caracterizado por el carpopodio escasamente desarrollado y difiere mayormente de la casi simpátrica *C. paneroi* B.L. Turner en sus hojas verdes (vs. nagruzcas) en seco, involucro de ca. 4 (vs. 7–8) mm de largo, ca. 20 (vs. 4 o 5) flores por cabezuela, corolas de ca. 4 (vs. 7–8) mm de largo, aquenios glabros de ca. 2 (vs. diminutamente glandulares y de 4–4.5) mm de largo.

ABSTRACT

Critonia guerrerensis Rzed., **sp. nov.**, is described as new and illustrated on the basis of a specimen collected in the higher part of the Sierra Madre del Sur in the state of Guerrero, Mexico. The new species belongs to the group characterized by a poorly developed carpopodium and differs from the almost sympatric *C. paneroi* B.L. Turner in its green (vs. drying blackish) leaves, involucre ca. 4 (vs. 7–8) mm long, ca. 20 (vs. 4 or 5) flowers per head, corollas ca. 4 (vs. 7–8) mm long, achenes glabrous and ca. 2 mm long (vs. glandular-atomiferous and 4–4.5 mm).

Al revisar materiales colectados en años anteriores, se encontraron plantas de una especie novedosa, que se describe a continuación.

CRITONIA GUERRERENSIS Rzed., **sp. nov.** **TIPO: MÉXICO. Guerrero.** Mpio. General Heliodoro Castillo (antes Tlacotepec): Ca. 2 km al NE de Campamento El Gallo, estribaciones suroccidentales del Cerro Teotepec, aprox. 17º 28' N, 100º 13' W, alt. 2650 m, ladera granítica con vegetación de bosque mesófilo de *Pinus, Abies, Clethra* y *Quercus,* arbusto de 3 m de alto: flores de color morado pálido, flores aromáticas, 27-29 ene 1963, *J. Rzedowski* y *R. McVaugh 129* (holotipo: IEB; isotipo: MICH, otros isotipos por distribuirse). Figura 1.

Frutex ca. 3 m altus; folia opposita petiolis 0.5-2 cm longis, laminis late lanceolatis vel ellipticis 6-17 cm longis, 2-5 cm latis, apice longe acuminatis, basi plerumque cuneatis, margine serratis, pinnatinervatis membranaceis pellucido-punctatis, in siccitate viridibus, supra fere glabris, subtus praecipue ad nervios puberulis; inflorescentia terminalis foliacea paniculiformis, paniculis partialibus hemisphaericis 3-4 cm diametro modice compactis, capitulis 16-24; involucra anguste campanulata ca. 4 mm longa 3-4-seriata gradata, phyllariis ca. 15 apice plerumque rotundato, receptaculo plano glabro, floribus ca. 20 per capitulum; corollae tubulosae ca. 4.5 mm longae dilute purpureae; achaenia ca. 2 mm longa atrobrunnea vel fere nigra glabra, carpopodio parum conspicuo; pappus ca. 25 setis rigidis ca. 4 mm longis albis.

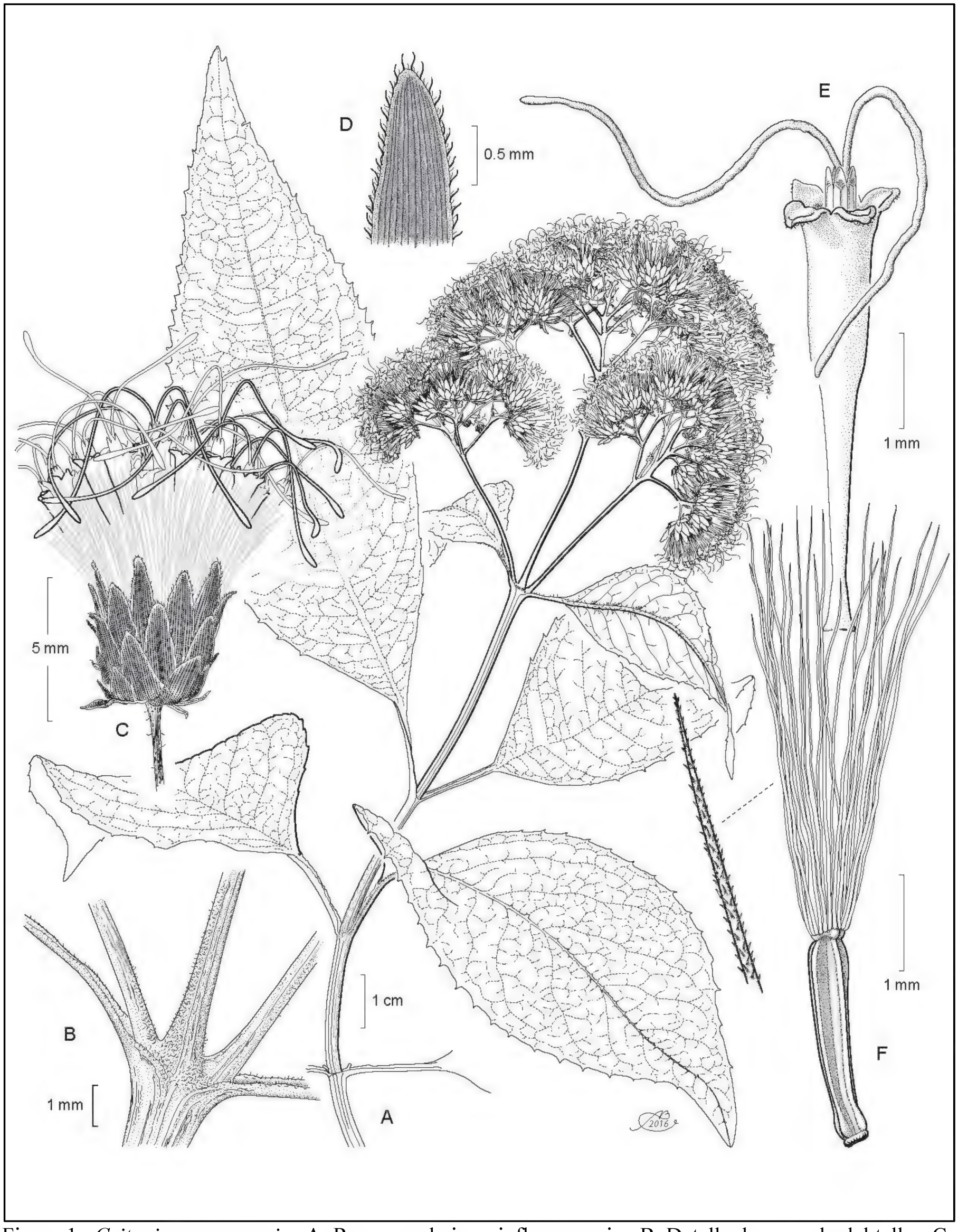

Figura 1. *Critonia guerrerensis.* A. Rama con hojas e inflorescencia. B. Detalle de un nudo del tallo. C. Cabezuela. D. Porción superior de una bráctea del involucro. E. Corola y ramas del estilo. F. Aquenio y vilano. Ilustrado por Alfonso Barbosa.

Arbusto de ca. 3 m de alto; ramas juveniles hexagonales, las maduras teretes y someramente lineado-estriadas, las más gruesas de color café y glabras, las más jóvenes moradas y a menudo algo pubérulas con pelos crespos diminutos por lo general dispuestos en líneas; hojas opuestas, peciolos de 0.5 a 2 cm de largo, con el mismo tipo de pubescencia, láminas anchamente lanceoladas a elípticas, de 6 a 17 cm de largo, de 2 a 5 cm de ancho, largamente acuminadas y con frecuencia algo falcadas en el ápice, cuneadas o a veces redondeadas en la base, margen serrado con 2 a 3 dientes mucronados por cm, aunque entero o casi entero en la porción basal, pinnatinervadas, de textura membranácea, irregular y por lo común esparcidamente pelúcido-punteadas, verdes con el secado en ambas caras, glabras o casi glabras en el haz, pubérulas principalmente a lo largo de las nervaduras en el envés, con pelos similares a los de los tallos; inflorescencia en forma de especie de panícula foliosa terminal, compuesta en realidad de una panícula propiamente apical y de dos a cuatro axilares originadas a partir de las hojas superiores, cada panícula parcial de forma hemisférica, de 3 a 4 cm de diámetro y 1.5 a 2 cm de alto, moderadamente compacta, con 16 a 24 cabezuelas, pedúnculos principales de 1 a 1.5 cm de largo, glabros al igual que los demás ejes de la inflorescencia, pero a menudo con algunos pelillos en las axilas de las ramificaciones, pedicelos de 2 a 5 mm de largo, brácteas ausentes; involucros angostamente campanulados, de ca. 4 mm de largo, sus brácteas ca. 15, graduadas en 3 a 4 series, las exteriores ovadas, las interiores oblongas, mayormente cafés con el margen pajizo, por lo general redondeadas en el ápice, con numerosas costillas, aunque éstas no siempre muy evidentes, glabras o casi glabras por fuera, todas menos las interiores densamente ciliadas en los márgenes, estas últimas pronto caedizas; receptáculo plano, glabro, flores ca. 20 por cabezuela, aromáticas; corolas tubulosas, de ca. 4.5 mm de largo, moradas pálidas, pubérulas en el extremo distal, estilos filiformes, sobresalientes casi otro tanto del largo de la corola; aquenios 5-angulados, de ca. 2 mm de largo, cafés oscuros a casi negros, con el carpopodio muy poco conspicuo, blanco, glabros, vilano de ca. 25 cerdas rígidas, blancas, de ca. 4 mm de largo.

La especie solo se conoce de la localidad tipo, ubicada el las laderas del cerro Teotepec, que es la mayor elevación (3550 m s.n.m.) del estado de Guerrero, ubicada en la Sierra Madre del Sur. De esta montaña ya se han descrito numerosas especies nuevas, con frecuencia estrechamente endémicas, como *Arnicastrum guerrerense* Villaseñor, *Castilleja venusta* Rzed., *Macromeria hintoniorum* B.L. Turner (ahora conocida como *Lithospermum turneri* J.I. Cohen), *Miconia portogallensis* de Santiago & Michelang., *Miconia teotepecensis* de Santiago (Melastomataceae), *Microspermum hintonii* Rzed., *Oreoweisia mexicana* H. Rob., *Romanschulzia guerrerensis* Bustamante & Fonseca, *Utricularia petersoniae* P. Taylor, *Vaccinium wilburii* Almeda & Breedlove, *Valeriana bryophila* Barrie, *Valeriana gallinae* Barrie, *Verbesina alcabrerae* Rzed. También se cuenta con un substancial listado florístico de la región, que incluye la descripción de la vegetación del área (Velázquez y Domínguez Licona 2003).

De particular interés es la circunstancia de que hace relativamente poco tiempo Turner (1996) describió *Critonia paneroi* con base en material colectado también en la Sierra Madre del Sur de Guerrero (25 km al S de Carrizal de Bravo, sobre la carretera a Puerto del Gallo), en lugar distante solamente pocos kilómetros de la localidad de *C. guerrerensis*. Como puede verse en el Cuadro 1, se trata evidentemente de taxones diferentes, aunque vinculados entre sí, pues pertenecen al pequeño conjunto del género caracterizado por el escaso desarrollo del carpopodio (Turner 1997). En tal contexto se incluyen además en la comparación otras dos especies de *Critonia*, de la misma afinidad. Éstas son de relativamente amplia distribución geográfica, pero se registran asimismo del estado de Guerrero, a mencionar: *C. hebebotrya* DC. y *C. hospitalis* (B.L. Rob.) King & Rob.

	C. guerrerensis	**C. paneroi**	**C . hospitalis**	**C. hebebotrya**
Porte	arbusto	árbol	árbol o arbusto	árbol o arbusto
Ramas	con 6 lados en la juventud	teretes	con 4 a 6 lados en la juventud	con 6 lados en la juventud
Hojas				
color en seco	verde	negruzco	verde	negruzco
forma	anchamente elíptico-lanceolada a elíptica	elíptica a ovada	elíptica a lanceolada	ovada, elíptica o lanceolada
margen	serrado	oscuramente crenulado	calloso, casi entero	serrulado a crenulado
Involucro				
largo en mm	ca. 4	7-9	5-6	4-4.5
Flores/cabezuela	ca. 20	4 o 5	5 o 6	5
Corola				
largo en mm	ca. 4.5	7-8	3-4	3-4
Aquenios				
largo en mm	ca. 2	4-4.5	2.5-3	2-2.5
pubescencia	ausente	diminutamente glandular	ausente a densa	cerdosa
Altitud conocida				
en m	2650	2400	800-2500	200-1600

Cuadro 1. Principales diferencias entre *Critonia guerrerensis*, *C. paneroi*, *C. hospitalis,* y *C. hebebotrya*.

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ROMULEA ROSEA (IRIDACEAE) NEW FOR THE ARKANSAS FLORA

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ABSTRACT

Romulea rosea (L.) Ecklon is reported here for the first occurrence outside of cultivation in Arkansas and in the eastern USA. In 2009, a small population of naturalized *R. rosea* plants was discovered growing in a lawn in the city of Arkadelphia, Clark County. This population slowly has increased in size over the past decade but has not spread beyond the immediate site of discovery. Photographs of *R. rosea* in habitat and keys to identification of the similar genera of Iridaceae currently known from the Arkansas flora are provided.

In 2009, a small, naturalized population of *Romulea rosea* (L.) Ecklon (rosy sandcrocus, onion grass) was discovered in Clark Co., Arkansas (Figs. 1–2). This genus and species previously have not been documented in the Arkansas flora outside of cultivation (Smith 1994; Arkansas Vascular Flora Committee 2006; Gentry et al. 2013). The plants initially were discovered growing in an unkempt lawn in a residential area in the city of Arkadelphia. The population has persisted and slowly increased in size since 2009, consisting of six plants as of 2020. To our knowledge, the population has not spread beyond the initial area of discovery. No cultivated plants of *R. rosea* were present in the vicinity of the population. Although the origin of the population is unknown, establishment is presumed to be via seeds or corms that were introduced to the site via contaminated soil or horticultural materials. Increases in the number of individuals appears to be via seeds, as most of the plants in the population are spaced too widely for production vegetatively from offsets. The population will continue to be monitored.

Voucher specimen. **Arkansas.** Clark Co.: Arkadelphia, N of O'Connell St. and 19th St. intersection, small, naturalized population of about six plants of unknown origin growing in unkempt lawn area of residence, not cultivated or persisting from cultivation, 23 Mar 2020, *Serviss 8721* (HEND).

Romulea rosea is a cormose perennial that is native to South Africa (de Vos 1983; Manning & Goldblatt 2001; Goldblatt 2002). It sometimes is cultivated in the USA as an ornamental for its small but showy, pink flowers (Bailey & Bailey 1976). It previously has been documented in the USA only from California, where it is naturalized in several counties, and Texas (Goldblatt 2002; Singhurst et al. 2009; Kartesz 2015; USDA, NRCS 2020), making our record apparently the first documented occurrence of this genus and species outside of cultivation in the eastern USA. The plants naturalized in North America correspond to *R. rosea* var. *australis* (Ewart) M.P. de Vos, which has become a common weed of lawns, pathways, and roadsides in Australia (Goldblatt 2002).

Figure 1. *Romulea rosea* naturalized in Clark Co., Arkansas. The naturalized population consists of about six plants and is present in a residential lawn in Arkadelphia — three flowering plants can be seen in the photograph.

Figure 2. (A–D) *Romulea rosea* plant and habit (from naturalized plants in Clark County). (A) Close-up of flower; notice the yellow throat, indicating that it is *R. rosea* var. *australis*. (B) Close-up of leaves; notice the two grooves on either side of the large midvein — this character and the plant's small size help to distinguish it from other Iridaceous species in Arkansas. (C) Side view of flower and scape — the flowering scape and leaves originate below ground from a small corm. (D) Lower stem, corm, and roots.

In Arkansas, *Romulea rosea* possibly could be confused with *Crocus* (if plants are sterile), which only recently has been documented from the state's flora (Serviss et al. 2016). *Romulea* can be reliably distinguished from *Crocus* using the following key (modified from Sell & Murrell 1996).

1. Leaves flat, channeled, and with a white line on the adaxial surface; flowers yellow to orange ..... **Crocus flavus**
1. Leaves subterete, with 4 grooves (2 on each surface, 1 on either side of the midrib), without white line; flowers pink to magenta with yellow throat ..... **Romulea rosea**

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ERIGERON DECRESCENS (ASTERACEAE: ASTEREAE), A NEW SPECIES FROM SOUTHEASTERN ARIZONA

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ABSTRACT

Erigeron decrescens Nesom & Roll, **sp. nov.**, is described from desert grassland near the Pat Hills of Cochise Co., Arizona. It is hypothesized to be derived from the *Erigeron divergens* complex and grows in close association with both an expression of typical annual *E. divergens* and the perennial *Erigeron incomptus*. Plants of *E. decrescens* are set apart especially by their diminutive size — the stems are only 2–3.5 cm tall and the ray corollas are conyza-like, barely extending beyond the involucre.

In an ongoing floristic inventory of the Pat Hills desert grassland of Cochise County (Roll 2018), a distinctive population of *Erigeron* has been discovered, documented here as a previously undescribed species.

ERIGERON DECRESCENS Nesom & Roll, **sp. nov.** **TYPE**: **Arizona**. Cochise Co.: Pat Hills, ca. 30 km (by air) SE of Willcox in the Sulphur Springs Valley, W of Chiricahua Mts, [see pin marking on Fig. 3], desert grassland dominated by *Prosopis velutina, Isocoma tenuisecta, Erigeron incomptus, Eragrostis lehmanniana, Sporobolus wrightii, Hilaria mutica*, snd *Hopia obtusa*, at the edge of a periodically wet depression in a small draw at the bottom of an andesitic hillside, 4540 ft, 22 Apr 2019, *C.M. Roll 2865* (holotype: ARIZ; isotype: PH).

Similar in vestiture, leaf shape, and fruit morphology to plants of the *Erigeron divergens* complex but different in its much shorter stems, densely strigose stem vestiture, smaller heads with ray corollas barely longer than the involucre, and deeply cup-shaped involucres.

Winter annuals from a thickened taproot and multicipital, highly condensed caudex. **Stems** multiple from the base, erect to ascending, 2–3.5 mm, densely and loosely strigose to strigose-villous with ascending hairs, minutely glandular. **Leaves** mostly basal, persistent, blades obovate-spatulate, basally attenuate to a narrow petiole often as long as the blade, 2–4.5 cm long, blades 3–15 mm wide, margins entire or with 1–2(–3) pairs of teeth or lobes, faces finely and evenly hirsute to loosely strigose-hirsute, minutely glandular; cauline leaves linear. **Heads** 1 per stem, at the level of the leaves or slightly above or below, buds erect. **Involucres** deeply cupulate, 8–10 mm wide (pressed). **Phyllaries** in 2(–3) series of subequal length, linear-lanceolate, 3–3.5 mm long, hirsute to hirsute-villous with long, multicellular, flattened hairs, minutely glandular. **Ray florets** ca. 80–150; corollas white, drying white or becoming purplish abaxially, ca. 3.5 mm long, tube with prominent, long, patent, 2-seriate hairs, laminae 0.1–0.2 mm wide. **Disc corollas** ca 1.5 mm long, throats not indurate or inflated. **Achenes** oblong, slightly compressed, ca. 0.8 mm long, 2-nerved, faces sparsely strigose; pappus of 8–10 fragile bristles 1 mm long, with a minute, fimbriate outer corona.

Erigeron decrescens is currently known only from the type locality, where plants are abundant around the depression. Flowering begins in late March and continues into May.

The plants appear to be winter annuals, germinating with the rains of late fall and early winter and continuing to grow with the extra moisture on the margins of the wet depression, an unusual desert grassland habitat. Other annuals around the depression include these: *Veronica peregrinus*, *Androsace occidentalis*, *Calandrinia ciliata*, *Myosurus minimus*, *Descurainia pinnata*, *Spermolepis latiflora*, *Verbena bracteata*, *Plantago virginica*, *Eryngium heterophyllum*, and *Erigeron divergens*.

Plants of *Erigeron divergens* Torr. & Gray at the type locality are annual, with multiple decumbent-ascending stems from the base and solitary heads topping unbranched stems (e.g., Fig. 2; see Nesom 2015). The perennial *E. incomptus* A. Gray (with woody caudex and taproot) also is abundant at the site and generally in the Pat Hills area. Intermediates between *E. decrescens* and the other two species are not evident. Among the three species, flowering in the Pat Hills begins first in *E. incomptus*, followed by *E. divergens*, and then by *E. decrescens*.

Erigeron decrescens may be a native South American "conyzoid" species, perhaps arriving in Arizona via the cattle industry, but if so it apparently has not been named there. Or it may instead be closely related to the native *Erigeron divergens* complex. The distinctive features of these plants primarily reflect reductions in length — especially the shorter stems and shorter ray corollas — and it seems reasonable to suspect that the striking transition in aspect might be mediated by relatively simple genetic changes.

Figure 1. *Erigeron descrescens*, from the type collection.

Figure 2. *Erigeron descrescens*, from the type collection.

Figure 3. Cochise Co., Arizona, with type locality of *Erigeron decrescens*. Plants corresponding to *E. decrescens* were not documented by Makings (2006) along the San Pedro River. Google Earth map.

Figure 4. Type locality of *Erigeron descrescens*. Photo by Chris Roll, 14 February 2020.

Figure 5. *Erigeron decrescens* at the type locality. Photo by Chris Roll, 22 April 2019.

Figure 6. *Erigeron divergens* (left) and *E. decrescens* (right), at the type locality of *E. decrescens*. Photo by Chris Roll, 22 April 2019.

Figure 7. *Erigeron decrescens* at the type locality. Photo by Chris Roll, 22 April 2019.

Figure 8. *Erigeron descrescens*, vestiture. Leaf (top) and nodal area (bottom).

Figure 9. *Erigeron descrescens*, young and mature heads.

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UNA NUEVA ESPECIE DE *PINGUICULA* (LENTIBULARIACEAE) DE NUEVO LEÓN, MÉXICO

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RESUMEN

Se describe e ilustra **Pinguicula bustamanta** Zamudio & Nevárez, **sp. nov.**, a partir de material procedente de la Sierra de Gomas, en el municipio de Bustamante, Nuevo León, México. La nueva especie se ubica en *Pinguicula* secc. *Isoloba* subsecc. *Agnatiformis*, dentro de esta sección es más parecida a *Pinguicula lilacina*, con la que se compara. Adicionalmente se proporcionan una clave para diferenciar las especies mexicanas reconocidas en esta sección y un mapa de distribución.

ABSTRACT

Pinguicula bustamanta Zamudio & Nevárez, **sp. nov.**, is described and illustrated based on specimens collected on the Sierra de Gomas of Nuevo León, Mexico. The new species is situated in *Pinguicula* sect. *Isoloba* subsect. *Agnatiformis* and is compared with *Pinguicula lilacina*, which is the most similar species. A key to identify the Mexican species of the section and a distribution map are provided.

Exploraciones realizadas en la parte norte del estado de Nuevo León para el estudio de la distribución ecológica de la herpetofauna de la Sierra de Gomas, también conocida como Sierra de Bustamante (tesis doctoral del segundo autor), condujeron, de manera incidental, al descubrimiento de una población de *Pinguicula* muy parecida a *Pinguicula lilacina*. Al revisar el material disponible en cultivo y observar las plantas en el campo se llegó a la conclusión de que se trata de una nueva especie.

PINGUICULA BUSTAMANTA Zamudio & Nevárez, **sp. nov. TIPO: MÉXICO. Nuevo León.** Mpio. Bustamante: Sierra de Gomas, alt. 900 m, 27 Mayo 2018, *S. Zamudio*, *M. Nevárez*, *y R. Quirino 17370* (holotipo: UAMIZ; isotipos: CIIDIR, ENCB, IBUG, MEXU). Figs. 1, 2, y 3.

Herbae perennis; rhizoma simplex breve radicibus adventitiis filiformibus numerosis; folia radicalia rosulata membranacea 4-6(8) obovata vel oblonga rotundata integerrima margine vix involuta basin versus abrupte cuneatim angustata superne glandulis sessilibus dense et glandulis stipitatis disperse vestita, inferne glandulis stipitatis disperse vestita 11-30 mm longa 5-17 mm lata; hibernacula nulla; pedicelli 1-8 erecti filiformes (30)40-80 mm alti glandulis stipitatis dense obsiti; flores 10-14 mm longi (calcari incluso); calyx bilabiatus extus glandulis stipitatis disperse obsitus, labium superum usque ad basim trilobum lobis triangulatis vel lanceolatis acutiusculis vel obtusis, labium inferum usque ad dimidium bilobum lobis triangulatis acutiusculis vel obtusis; corolla subisoloba alba vel lilacina marginata fauce lutea extus glandulis stipitatis obtecta lobis oblongis vel ample oblongis rotundatis vel truncatis 3-5 mm longis 3-5 mm latis; tubus subcylindricus 5-6 mm longus 4-5 mm latus cum palato et cymatio palati intus disperse pilosus pilis longis clavate capitatis infra palati pilis similibus in striistriabus retro conversis; palatum semilentiforme ± 2 mm longum 1-2 mm latum luteum pilis tenuibus brevibus dense obtectum; calcar breve cylindricum obtusum sursum versum 2-4.5 mm longum

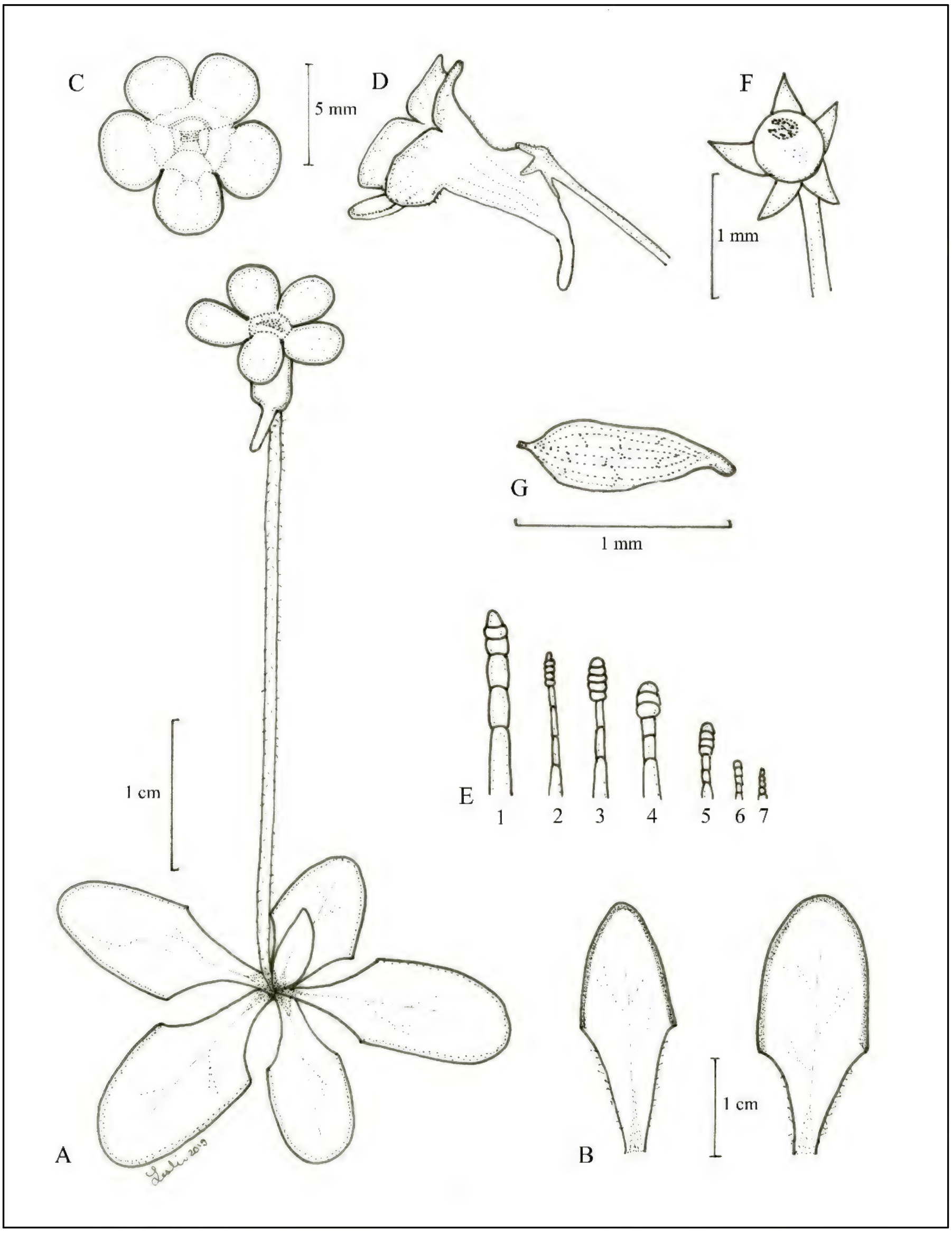


Figura 1. *Pinguicula bustamanta*. A. Planta con flor. B. Variación en la forma de las hojas. C. Vista frontal de la flor. D. Vista lateral de la flor. E. Pelos glandulares de la corola, 1-4 Pelos del tubo, 5-6 Pelos del paladar, 7 Pelos del espolón. F. Fruto. G. Semilla.

cum tubo angulum obtusum formans; stamina ± 1.5 mm longa; antherae ± 0.5 mm longae; ovarium subglobosum glandulis stipitatis modice dense obsitum; stigma bilabiatum labium inferum papillatum; capsula subglobosa 2-3 mm diametro; semina numerosa fusiformia 0.8-1 mm longa 0.4-0.5 mm lata, striata.

Planta herbácea perenne; **rizoma** simple, corto, con numerosas raíces adventicias filiformes; **hojas** membranáceas, 4 a 6(8), agrupadas en una roseta basal, lámina obovado-espatulada a oblongo-espatulada, de 11 a 30 mm de largo, por 5 a 17 mm de ancho, ápice redondeado, base abruptamente cuneada, margen involuto en la mitad apical, densamente glandular pubescentes en el haz con glándulas estipitadas menores de 0.5 mm y glándulas sésiles, esparcidamente glandular pubescente en el envés; roseta de invierno ausente; **pedúnculos** 1 a 4(8) por planta, de (30)40 a 80 mm de largo, densamente glandular pubescentes, glabrescentes hacia la base, con glándulas estipitadas menores de 0.5 mm; **flores** de 10 a 14 mm de largo (incluyendo el espolón); **cáliz** bilabiado, densamente glandular-pubescente en la cara externa, labio superior dividido casi hasta la base en tres lóbulos, triangulares a lanceolados, agudos a obtusos, de 1.5 a 2 mm de largo, por 0.8 a 1 mm de ancho, labio inferior dividido 1/2 a 2/3 de su longitud en dos lóbulos triangulares, agudos a obtusos, de 1 a 1.5 mm de largo, por 0.6 a 1 mm de ancho; **corola** subisoloba, blanca, a veces con el margen de los lóbulos lila, garganta amarilla, esparcidamente glandular estipitada por fuera, lóbulos oblongos a ampliamente oblongos, ápice redondeado a truncado, de 3 a 5 mm de largo, por 3 a 5 mm de ancho, **tubo** subcilíndrico, amarillo pálido en la parte superior, blanco en la base, en ocasiones con las venas tenuemente marcadas de color marrón claro, de 5 a 6 mm de largo, por 4 a 5 mm de ancho, cubierto densamente con tricomas simples, largos, claviformes o engrosados en el ápice dispersos y tricomas cortos subulados en la base, dentro del tubo los pelos se distribuyen en tres líneas, **paladar** semilentiforme, amarillo, de 2 mm de largo, por 1-2 mm de ancho, cubierto densamente con tricomas claviformes, más largos en los lados y muy cortos sobre la cima, **espolón** amarillo, cilíndrico, obtuso, de 2 a 4.5 mm de largo, se curva hacia arriba y forma un ángulo obtuso con el tubo; **estambres** ± 1.5 mm, antera 0.5 mm de largo, filamento curvo en la base, de ± 1 mm de largo; **ovario** subgloboso, de 1-1.5 mm de diámetro, densamente glandular pubescente, estigma bilabiado, el labio ínfero flabelado, papiloso en la cara interna, de 1.5 a 3 mm de largo, por 1 a 2 mm de ancho; **cápsula** subglobosa, de 2 a 3 mm de diámetro; **semillas** fusiformes, de 0.8 a 1 mm de largo, por 0.4 a 0.5 mm de ancho, superficie estriada.

Etimología

El epíteto específico deriva del municipio de Bustamante, Nuevo León, en donde se colectó la nueva especie.

Ecología

La nueva especie crece en cañadas, con taludes o laderas muy inclinadas de rocas calizas, con orientación NW, sombreadas y húmedas, con vegetación transicional entre el matorral submontano y el bosque bajo de encinos. Alt. 900 m.

La Sierra de Gomas, también conocida como Sierra de Bustamante se extiende por cerca de 60 km con rumbo noroeste-sureste, forma parte de un conjunto de sierras constituidas por rocas calizas del Cretácico, separadas de la Sierra Madre Oriental al noreste de Monterrey. Abarca parte de los municipios de Bustamante, Mina, Salinas Victoria y Villaldama (INEGI, 1986).

En la cima y laderas superiores de la Sierra de Gomas, predomina el clima semiseco-semicálido, con temperatura media anual entre 18 y 22 °C y precipitación anual entre 395 y 510 mm, con lluvias de verano, al que corresponde la fórmula BS_1hw.

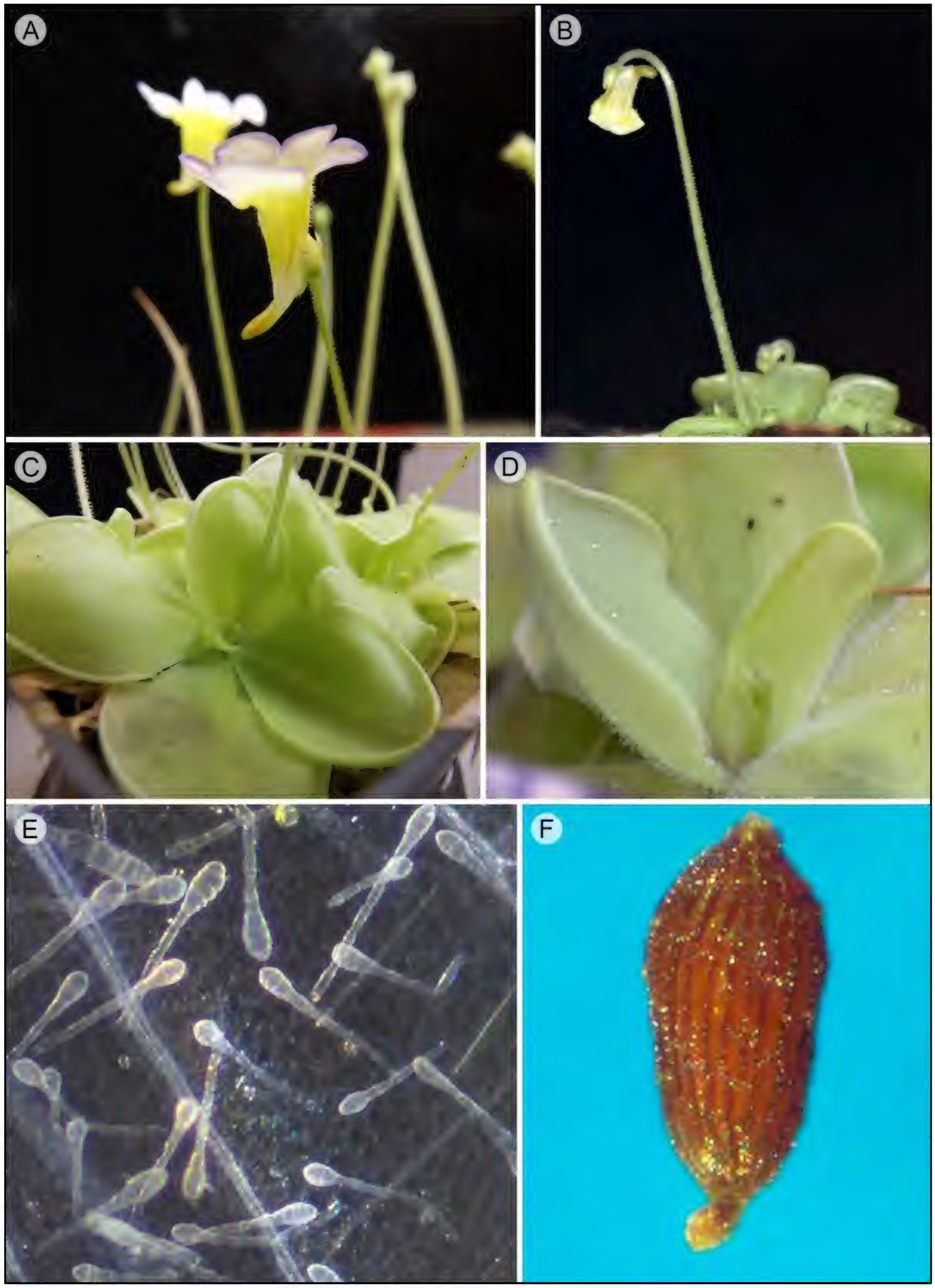


Figura 2. *Pinguicula bustamanta*. A. Flor vista de lado. B. Planta con flor inclinada por la noche. C. Roseta. D. Hojas jóvenes mostrando la pubescencia glandular en el envés. E. Tricomas del tubo de la corola. F. Semilla. Fotografías A, C, D Manuel Nevárez, B Julián Hernández, E y F Sergio Zamudio.

En la parte alta de las sierras se encuentran rodales aislados de un bosque bajo de encinos, en el que predominan *Quercus canbyi*, *Q. laeta*, *Q. polymorpha*, y *Q. rhysophylla*, asociados con *Arbutus arizonica*, *Carya illinoiensis*, *Juglans* sp., *Rhus andrieuxii*, *Ungnadia speciosa*, y *Vauquelinia corymbosa*. Mientras que en las laderas entre, 500 y 1100 m, se establece el matorral submontano, formado por arbustos subinermes de porte medio, así como por especies rosetófilas, las dominantes son: *Acacia amenthacea, A. berlandieri, Agave lechuguilla*, *A. scabra*, *A. tenuifolia*, *Amyris madrensis*, *Bernardia myricifolia*, *Cordia boissieri*, *Eysenhardtia texana*, *Forestiera angustifolia*, *Helietta parvifolia*, *Jatropha dioica*, *Leucophyllum frutescens*, *Neopringlea integrifolia*, *Rhus pachyrrhachis*, y *Schaefferia cuneifolia* (Canizales-Velázquez et al. 2009; Estrada-Castrillón et al. 2011).

Fenología

Se han colectado con flores en el mes de mayo, pero en cultivo se ha observado que las plantas producen flores y frutos durante todo el año y perduran por varios años, lo que permite afirmar que es una planta perenne. Se ha registrado un comportamiento curioso en las flores, durante el día las flores están erguidas sobre el pedúnculo, dirigidas hacia arriba para permitir la visita de los polinizadores, pero por la noche el pedúnculo se dobla y las flores permanecen inclinadas hasta la mañana siguiente (Fig. 2, A y B).

Discusión taxonómica

Pinguicula bustamanta pertenece a la secc. *Isoloba* subsecc. *Agnatiformis* Casper (1966), por la corola de tamaño intermedio (10-18 mm), con lóbulos casi iguales, enteros; tubo cilíndrico, con paladar y cima del paladar notorios, espolón corto; junto con *P. lilacina* Schltdl. & Cham., *P. pumila* Michx., *P. sharpii* Casper & Kondo, y *P. takakii* Zamudio & Rzed.

Dentro de este grupo la nueva especie es más parecida a *Pinguicula lilacina*, por el hábito y tamaño de las plantas; de ésta se puede separar por ser una planta perenne, que florece continuamente a lo largo del año (vs. anual y que florece de agosto a marzo), por las hojas con la base abruptamente cuneada (vs. base cuneada, angostándose gradualmente), por la presencia de pelos glandulares en el envés de las hojas (vs. pelos glandulares ausentes en el envés), por el cáliz con los lóbulos triangulares a lanceolados (vs. lóbulos oblongos), por la corola blanca con el tubo amarillo pálido, sin líneas púrpuras (vs. corola lila a blanca con el tubo amarillo con líneas púrpuras bien marcadas) y semillas de 0.8 a 1 mm de largo, con la testa estriada (vs. semillas de 0.5 a 0.6 mm de largo, con la testa alveolada). También existen diferencias en el hábitat que ocupan, ya que *P. bustamanta* crece sobre rocas calizas en ambientes con clima semiseco-semicálido, en la transición entre el bosque de encinos y el matorral submontano, a 900 m de altitud; mientras que *P. lilacina* crece en laderas de rocas calizas, graníticas o ígneas, en ambientes más húmedos, con vegetación de bosques de encino, pino y mesófilo de montaña, entre (500)950 y 2400 m (Tabla 1 y Figura 3).

Aunque *Pinguicula sharpii* y *P. takakii* también son similares en apariencia a *P. bustamanta*, son notoriamente de menor tamaño. Como en el caso anterior *Pinguicula bustamanta* se distingue de éstas además del tamaño, por la presencia de pubescencia glandular en el envés de las hojas, por la ausencia de líneas púrpuras o violáceas en el tubo de la corola, por los lóbulos del cáliz triangulares a lanceolados y por la semilla estriada (Tabla 1).

Figura 3. Comparación entre las flores de *Pinguicula bustamanta* (A) y *P. lilacina* (B). Fotografía A de Manuel Nevárez, fotografía B de Fernando Ribadavia.

Tabla 1. Comparación entre *Pinguicula bustamanta*, *P. lilacina*, *P. sharpii*, y *P. takakii*.

Caracteres	**P. bustamanta**	**P. lilacina**	**P. sharpii**	**P. takakii**
Hábito	Perenne	Anual	Anual-bianual	Perenne
Hojas forma	Obovadas a oblongas, base abruptamente espatulada	Obovadas, elípticas a ampliamente elípticas, base cuneada	Ampliamente obovado-espatulada	Obovadas, abruptamente cuneadas
Hoja, largo x ancho	11–30 x 5-17 mm	15–45 x 9–23 mm	14–18.5 x 11–17 mm	5–16 x 4–12 mm
Pubescencia glandular	En haz y envés	En el haz	En el haz	En el haz
Flor, tamaño	10–13 mm	(8)10–18 mm	3–9 mm	6–14 mm
Flor, color	Blanca, a veces con margen lila	Lila a blanca	Blanca o violácea	Violácea
Lóbulos labio sup. cáliz	Triangulares o lanceolados	Oblongos	Oblongos	Oblongos a triangulares
Lóbulos labio inf. cáliz	Triangulares, pubescente en ambas caras	Ovado-lanceolados	Oblongos	Triangulares
Tubo color	Amarillo con blanco en la base, sin líneas guindas o púrpuras, a veces con las venas tenuemente marcadas de color marrón claro	Amarillo con líneas púrpuras	Amarillo con líneas violáceas	Amarillo con líneas guindas
Espolón	2-4.5 mm	(1.5)2.5-4 mm	0.5-2.6 mm	2-3.5 mm
Semillas	0.8-1 x 0.4-0.5 mm	0.5-0.6 x 0.2 mm		0.4-0.5 x 0.2-0.3 mm
Semillas testa	Estriadas	Alveoladas		Reticuladas
Hábitat	Transición BQ-MS	BP, BQ, BMM	BP-Q	Matorral xerófilo (rosetófilo)
Altitud	900 m	(500)950-2000 m	1700 m	1350-1400 m
Floración	Todo el año en cultivo	Agosto-Febrero	Diciembre	Noviembre-Diciembre

Por su parte *Pinguicula pumila* del sureste de Estados Unidos, aunque es miembro de la subsección *Agnatiformis* es muy diferente de las especies mexicanas, no sólo por las características morfológicas sino también por sus preferencias ecológicas, pues crece en bosques de pinos o sabanas, sobre suelos arenosos húmedos, en la planicie costera del Golfo, en una franja altitudinal menor a 50 m; desde el sur de Carolina del Norte a Florida y las Bahamas, extendiéndose hacia el oeste hasta Luisiana y el este de Texas. Las rosetas están formadas por un mayor número de hojas ((8)12-16, o más), las que son obovado-oblongas y fuertemente involutas, los lóbulos del cáliz son lineares a oblongos, los lóbulos de la corola con frecuencia están emarginados, el tubo comúnmente tiene las venas marcadas de color morado y el paladar tiene una cima cónica o cilíndrica muy marcada. Adicionalmente el número cromosómico somático de *P. pumila* es 2n = 22, que difiere del de *P. lilacina* y *P. sharpii* que es 2n = 16 (Casper & Stimper, 2009).

Clave para el reconocimiento de las especies mexicanas de *Pinguicula* de la sección *Isoloba*, subsección *Agnatiformis*.

1. Flores blancas o lilas, tubo amarillo con líneas longitudinales lilas, moradas o púrpuras.
1. Flores blancas, tubo amarillo pálido sin líneas longitudinales lilas, moradas o púrpuras, crece en la transición entre matorral submontano y bosque de encino, en Nuevo León ..... **Pinguicula bustamanta**

2. Flores menores de 15 mm incluyendo al espolón.
2. Flores en general mayores de 15 mm incluyendo al espolón, crece en bosques de encino, mesófilo de montaña y pino, de amplia distribución en México y Centroamérica ..... **Pinguicula lilacina**

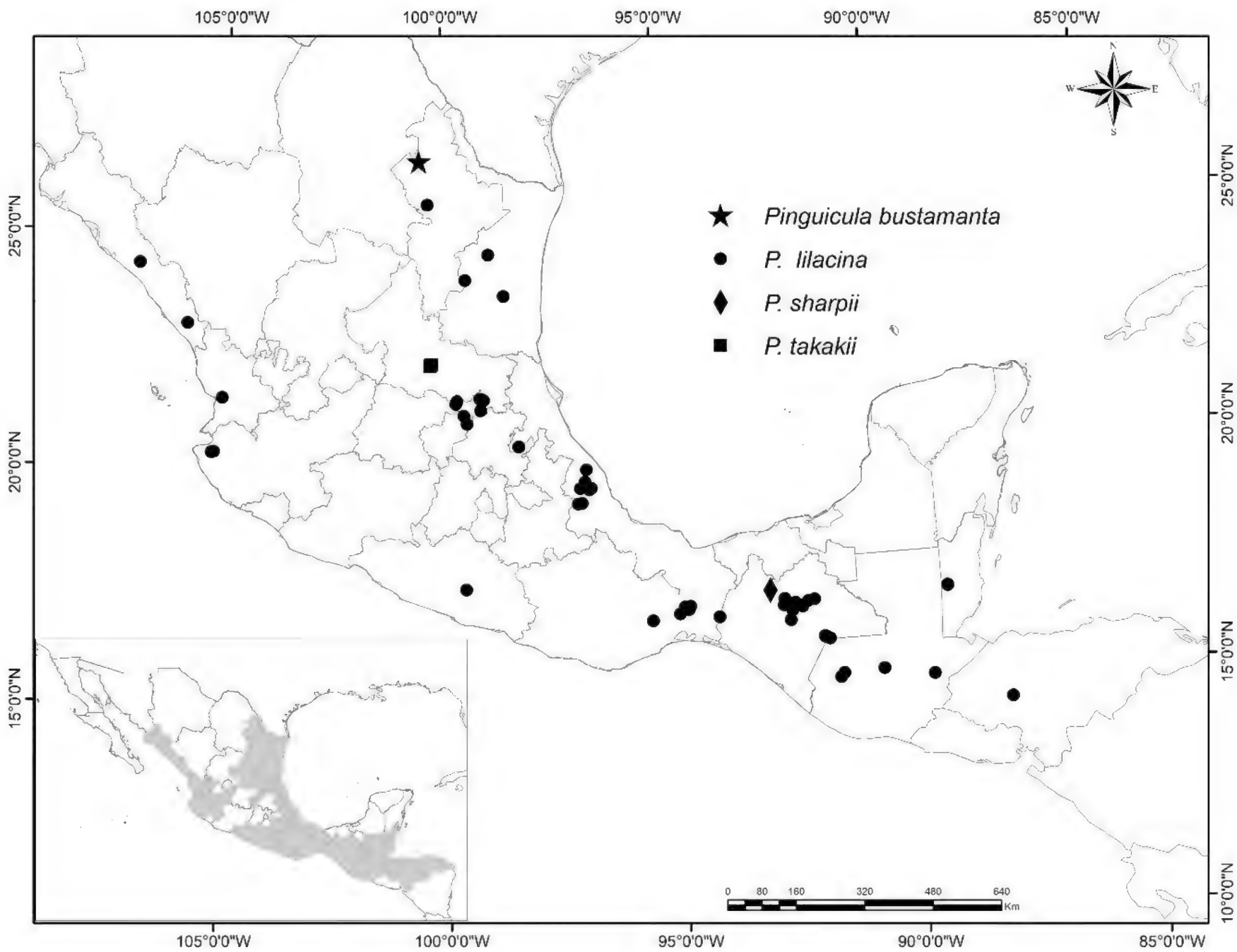
3. Plantas con flores lilas, de 6 a 14 mm de largo, crecen sobre suelos yesosos con vegetación de matorral rosetófilo, en San Luis Potosí ..... **Pinguicula takakii**
3. Plantas de flores blancas o lilas, de 3 a 9 mm de largo, crecen en bosque de pino-encino, en Chiapas ..... **Pinguicula sharpii**

La subsección reúne un conjunto de especies endémicas a México y norte de Centroamérica, la mayoría representan endemismos etrechos: *Pingucula sharpii* solo se conoce de la localidad tipo, en La yerbabuena, cerca de Pueblo Nuevo en el municipio de Jitotol, Chiapa y no se ha vuelto a colectar (Casper & Kondo, 1977). De igual forma *Pinguicula takakii* solo se conoce de los alrededores Buena Vista, en el municipio de Villa Juárez, San Luis Potosí (Zamudio y Rzedowski, 1986); mientras que *Pinguicula lilacina* se distribuye ampliamente, por un lado, desde Nuevo León y Tamaulipas en el oriente y por el otro desde Sinaloa en el occidente de México hasta Chiapas, extendiéndose hacia el sur hasta Belice, Guatemala y Honduras en Centroamérica (Casper, 1966; Zamudio, 2005). La existencia de *Pinguicula bustamanta* en la Sierra de Gomas al norte de Monterrey, marca el extremo norte de la distribución de este grupo en México (ver Mapa 1).

Es importante resaltar que las especies mexicanas de *Pinguicula,* sección *Isoloba*, subsección *Agnatiformis*, comparten un patrón morfológico similar, que sugiere que éstas se originaron de un ancestro común, a partir de poblaciones que quedaron aisladas geográficamente durante cientos o miles de años y que con el tiempo llegaron a diferenciarse por un proceso de especiación vicariante.

Precisamente, Casper & Stimper (2009) opinan que la existencia y distribución de las especies americanas de *Pinguicula,* sección *Isoloba*, subsección *Agnatiformis* se puede explicar si se toma en consideración los cambios climáticos ocurridos en el pasado; estos autores sugieren que los miembros del género *Pinguicula* con número cromosómico haploide x= 8 del Nuevo Mundo son los remanentes de antiguos linajes de especies de *Pinguicula* diploides que radiaron en los períodos más fríos del Pleistoceno extendiéndose hacia Cuba y Sudamérica, sin cambiar el nivel de ploidía. Según ellos, la presencia de especies muy cercanas o parecidas en el Nuevo Mundo con el número básico haploide x= 8 es la expresión de un antiguo período de especiación preglacial, que parece haber ocurrido por la diferenciación al nivel interno en los cromosomas, lo que dio como resultado una cadena o un mosaico

de especies vicariantes más o menos relacionadas. Es indudable que este proceso continuó en México en tiempos postglaciales, formando un conjunto de especies que se distribuyen desde el norte de México hasta Honduras (ver Mapa 1).



Mapa 1. Distribución geográfica de las especies mexicanas de *Pinguicula* secc. *Isoloba* subsecc. *Agnatiformis*. *Pinguicula bustamanta* (estrella); *P. lilacina* (punto); *P. sharpii* (diamante); *P. takakii* (cuadrado).

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NEW COMBINATIONS IN THE AMERICAN GENUS *ACMISPON* (FABACEAE: LOTEAE)

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ABSTRACT

Five new combinations are provided in *Acmispon* for western Mexico and the southwerstern United States: **Acmispon watsonii** (Vasey & Rose) Brouillet, **Acmispon argophyllus** var. **ornithopus** (Greene) Brouillet, **Acmispon strigosus** var. **tomentellus** (Greene) Brouillet, **Acmispon plebeius** (Brandeg.) Brouillet, and **Acmispon neomexicanus** (Greene) Brouillet.

While preparing the treatment of *Acmispon* for the Flora of North America north of Mexico project, I realized that some taxa from Mexico had not been transferred to this genus. New combinations are proposed here to fill this taxonomic gap. Meanwhile, Govaert (2018) corrected two species names published in the California flora (Brouillet 2010). Furthermore, two southwestern USA species not covered in this flora also require nomenclatural updating, as the epithets long used in *Lotus* (e.g., Isely 1981; Barneby 1989) do not have priority over those of synonyms included in the taxon concepts.

1. **Acmispon watsonii** (Vasey & Rose) Brouillet, **comb. nov.** Basionym: *Hosackia watsonii* Vasey & Rose, Proc. U.S. Natl. Mus. 11: 528. 1889 (as "Watsoni"). **TYPE**: **MEXICO**. **Baja California**. San Quintin Bay, Jan 1889, *E. Palmer 960* (holotype: US 48875 [barcode US00003563]). *Lotus watsonii* (Vasey & Rose) Greene, Pittonia 2: 149. 1890. *Syrmatium watsonii* (Vasey & Rose) Brand, Bot. Jahrb. Syst. 25: 232. 1898.

2. **Acmispon argophyllus** (A. Gray) Brouillet var. **ornithopus** (Greene) Brouillet, **comb. nov.** Basionym: *Hosackia ornithopus* Greene, Bull. Calif. Acad. Sci. 1: 185. 1886[1885]. **TYPE**: **MEXICO**. **Baja California**. Guadalupe Island, 19 Apr 1885, *E.L. Greeene s.n.* (holotype: CAS; isotypes: GH, NY!, US!). *Lotus argophyllus* (A. Gray) Greene var. *ornithopus* (Greene) Ottley, Univ. Calif. Publ. Bot. 10: 238, pl. 82. 1923. *Lotus argophyllus* subsp. *ornithopus* (Greene) P.H. Raven, Aliso 5: 326. 1963. *Lotus ornithopus* (Greene) Greene, Pittonia 2: 149. 1890. *Syrmatium ornithopus* (Greene) Greene, Bull. Calif. Acad. Sci. 2: 148. 1886.

3. **Acmispon strigosus** (Nutt.) Brouillet var. **tomentellus** (Greene) Brouillet, **comb. nov.** Basionym: *Lotus tomentellus* Greene, Pittonia 2: 140. 1890. **TYPE**: **MEXICO**. **Baja California**. Gulf of California, Los Angeles Bay, 22 Nov–20 Dec 1887, *E. Palmer 602* (holotype: NDG; isotype: K! [K000478364]). *Hosackia tomentella* (Greene) Brand, Bot. Jahrb. Syst. 25: 231. 1898. *Hosackia tomentella* (Greene) Abrams, Ill. Fl. Pacific States 2: 543. 1944 (isonym). *Lotus strigosus* (Nutt.) Greene var. *tomentellus* (Greene) Isely, Brittonia 30: 469. 1978.

Two of the three varieties of *Acmispon strigosus* have already been transferred to *Acmispon*: var. *strigosus* and var. *hirtellus* (Greene) D.W. Taylor (Taylor 2010). The third variety also requires a new combination. While varieties were not recognized in Brouillet (2010), the inclusion of material from Arizona fully justifies recognition of the three varieties discussed by Isely (1981).

4. **Acmispon plebeius** (Brandeg.) Brouillet, **comb. nov**. Basionym: *Hosackia plebeia* Brandeg., Proc. Calif. Acad. Sci., ser. 2, 2: 144. 1889. **TYPE**: **MEXICO**. **Baja California Norte**. El Rancho Viejo, 30 Apr 1889, *T.S. Brandegee s.n.* (holotype: UC [UC80720], photo!). *Lotus oroboides* var. *plebeius* (Brandeg.) Ottley Brittonia 5: 107. 1944. *Lotus plebeius* (Brandeg.) Barneby, Great Basin Naturalist 46: 257. 1986. *Ottleya plebeia* (Brandeg.) D.D. Sokoloff & Gandhi, Byull. Moskovsk. Obshch. Isp. Prir. Otd. Biol. 108: 41. 2003.

Hosackia rigida Benth. var. *nummularia* M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5: 633. 1895. *Anisolotus nummularius* (M.E. Jones) Woot. & Standl., Contr. U.S. Natl. Herb. 16 (4): 135. 1913. *Lotus nummularius* (M.E. Jones) Tidestr., Contr. U.S. Natl. Herb. 25: 303. 1925. *Lotus oroboides* var. *nummularius* (M.E. Jones) Isely, Brittonia 30: 468. 1978. *Lotus nummulus* Dayton, Proc. Biol. Soc. Washington 40: 119. 1927 (nom. illeg. nom. superf.).

Lotus oroboides var. *nanus* Isely, Brittonia 30: 468. 1978.

Lotus ramulosus M.E. Jones, Contr. W. Bot. 15: 138. 1929. *Lotus oroboides* var. *ramulosus* (M.E. Jones) Ottley, Brittonia 5: 107. 1944.

Lotus longebracteatus Rydb., Bull. Torrey Bot. Club 30: 254. 1903. *Anisolotus longebracteatus* (Rydb.) Rydb., Fl. Rocky Mts., 1063. 1917.

Barneby (1989) pointed out that the name *Lotus oroboides* (Kunth) Ottley (syn. of *Acmispon oroboides* (Kunth) Brouillet) only applies to plants present in the central Mexican highlands, though specimens extend north to the Sierra Madre Occidental in the states of Chihuahua and Sonora (pers. observ.). The distributions of *A. plebeius* and *A. oroboides* appear essentially disjunct, the former being present in Mexico only in Coahuila and Baja California.

5. **Acmispon neomexicanus** (Greene) Brouillet, **comb. nov.** Basionym: *Lotus neomexicanus* Greene, Pittonia 2: 144. 1890 (as "Neo-Mexicanus"). **TYPE**: **USA**. [**New Mexico**]. Santa Rita del Cobre, 1877, *E. Greene 49719* (holotype: NDG photo!, Ottley 1944]. *Anisolotus neomexicanus* (Greene) A. Heller, Muhlenbergia 8: 60. 1912. *Hosackia neomexicana* (Greene) Brand, Bot. Jahrb. Syst. 25: 229. 1898.

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Anisolotus mollis A. Heller, Muhlenbergia 8: 60. 1912. *Hosackia mollis* Greene, Bull. Calif. Acad. Sci. 1: 185. 1886[1885] (nom. illeg.). *Lotus mollis* Greene Pittonia 2: 143. 1890 (nom. illeg.). *Ottleya mollis* (A. Heller) D.D. Sokoloff & Gandhi, Byull. Moskovsk. Obshch. Isp. Prir. Otd. Biol. 108: 41. 2003.

Although Barneby (1989) included the name *Lotus neomexicanus* in synonymy of *L. plebeius* (syn. of *Acmispon plebeius*), I concur with the interpretation provided by Ottley (1944) that it is part of the taxon concept of *L. greenei*, after examination of the type photo she provides. The specimen mentioned as probable type by Ottley is the only specimen she saw that corresponds with the description in the protologue, which mentions "near Silver City in the spring of 1877." Santa Rita del Cobre, a ghost village, is located 15 miles east of Silver City, which fits reasonably well with "near Silver City." This specimen is the holotype of *L. neomexicaus* (although Barneby 1989 mentions lectotype).

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PERIPHYTON CHARACTERISTICS ARE A MORE ACCURATE INDICATOR OF TROPHIC STATUS RELATIVE TO WATER-COLUMN CHARACTERISTICS OF A SHALLOW LAKE IN DUNBAR CAVE STATE PARK IN MIDDLE TENNESSEE

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ABSTRACT

Swan Lake in Dunbar Cave State Park is impaired by nutrient enrichment as evidenced by nuisance biomass levels of macrophytes and mats of surface algae. Concentrations of total phosphorus and total nitrogen of water were below those expected in a eutrophic environment, most likely due to high demand. Other characteristics of the water column including chlorophyll *a* concentration, biochemical oxygen demand, and primary production were also below levels expected in a eutrophic environment and presumably reflect the low concentration of phosphorus and nitrogen of the water. Periphyton characteristics accurately indicate the eutrophic status of the lake and include a high concentration of benthic chlorophyll *a*, high concentration of ash-free dry mass of benthic organics, and a high relative abundance of soft algal and diatom taxa listed as eutrophic indicators. The results indicate that (1) periphyton characteristics best characterize the trophic status of Swan Lake relative to water-column characteristics and that (2) assessment and monitoring of eutrophic lentic habitats should include measurements of periphyton characteristics.

Phosphorus (P) enrichment frequently increases primary production and is a major cause for the degradation of aquatic communities worldwide (Chonova et al. 2019). High rates of primary production, high concentrations of chlorophyll (chl) *a,* and changes of organism composition are hallmarks of eutrophication (Harris and Piccinin 1977). The primary objectives of this research were to characterize the water quality and biological integrity of Swann Lake in Dunbar Cave State Park such that changes can be monitored. We used multiple approaches to achieve the objectives including determinations of (1) nutrient concentrations of water, (2) pigment concentrations of water and periphyton, (3) biochemical oxygen demand of water, (4) primary production on artificial substrates, and (5) composition of benthic soft-algal and diatom assemblages.

The above ground origin of Swan Creek is the entrance to Dunbar Cave in Dunbar Cave State Park in Clarksville, Tennessee. The creek is dammed approximately 0.3 km downstream of the cave entrance forming Swan Lake. The lake is approximately 35 ha and averages approximately 3 m deep. Swan Creek is part of the Lower Cumberland River Watershed which is in the Western Pennyroyal Karst (71e) and Western Highland Rim (71f) Level IV Ecoregions. The geologic base of the watershed is Mississippian-age limestone and includes some chert, shale, siltstone, sandstone, and dolomite. The soils are a thin loess mantle, highly erodible, and very fertile (Baskin et al. 1997). Forests are Western Mesophytic and consist largely of *Quercus* and *Carya* species. Over 50% of the Lower Cumberland River Watershed is used to produce agriculture products including tobacco, corn, soybean, and livestock (TDEC 2012). The cumulative effects of erosion, agricultural runoff, livestock access to streams, and poorly functioning sewage systems result in poor quality water in most of the tributaries in the watershed, including Swan Creek. The negative impact of eutrophic conditions of Swan Lake is obvious by the nuisance biomass levels of the aquatic macrophyte *Myriophyllum spicatum* L. and surface algal mats.

Methods

Water-column characteristics of Swan Lake were determined on September 9, 2019, following the methods described by Lebkuecher et al. (2018a). Photosynthetic photon flux density (PPFD) was measured at the surface and at 0.25-m depths at 2 locations (2 replicates) with a spherical underwater quantum sensor coupled to a Li-Cor quantum meter (Li-Cor Cooperate, Lincoln, Nebraska). These data were used to calculate the vertical extinction coefficient of light (n"; Lind et al. 1992): n" = (ln $PPFD_{surface}$ - ln $PPFD_{depth}$)/depth. The value of n" is an expression of the PPFD-depth slope on a logarithmic axis and is largely a function of turbidity; the higher the n" value, the greater the vertical extinction rate of light as it penetrates the water column. Concentrations of total phosphorus (TP) and total nitrogen (TN) of water samples collected with a Van Dorn sampler at 0.25 m depth were determined using a Lachat QuickChem 8500 Flow Injection Analyzer. [TP] was determined using the persulfate-digestion and the ascorbic-acid method (Baird et al. 2017). [TN] was determined by the persulfate-digestion and cadmium-reduction method (Baird et al. 2017).

Concentration of chl *a* concentration and turbidity of the water at a 0.25-m depths at six different locations (six replicates) were determined using a portable fluorometer and nephelometer (AlgaeChek Ultra, model RS232, Modern Water Incorporated, New Castle, Delaware). The fluorometer measures the intensity of fluorescence at 685 nm emitted from chl *a* upon excitation by low emission diodes (470 nm). The nephelometer measures the concentration of suspended particulates expressed as nephelometric turbidity units calculated from the intensity of scattered light reflected from a source beam due to particles in the water.

Primary production of the water was determined using a periphytometer holding glass microscope slides (25- by 75-mm) vertically 5 cm below the surface. The periphytometer was deployed on Aug. 30, 2019, and retrieved Sept. 9, 2019. No significant rainfall occurred during the deployment and most days were partly cloudy. Periphyton were removed from both sides of 12 slides using a razor blade (two slides per six replicates) into 100 mL of deionized water. The periphyton were suspended in water by swirling and concentrations of chl *a* determined using the AlgaeChek portable fluorometer probe described above.

The effect of organic matter in the water column on oxygen consumption by microorganisms was estimated by the biochemical oxygen demand 5-day assay (BOD_5 assay) as described by Baird et al. (2017). Water samples were retrieved from a depth of 0.25 m using a Van Dorn sampler. Samples were transferred to two borosilicate-glass bottles with ground-glass stoppers. Initial dissolved oxygen (DO) concentration was determined using a portable DO meter (model MW600, Milwaukee Instruments Incorporated, Rocky Mount, North Carolina). The bottles were incubated for 5 days in darkness at 25 ^{O}C and the concentration of DO consumed recorded as BOD_5 (mg DO $\cdot$ $L^{-1} \cdot 5$ d^{-1}).

Periphyton chl *a* concentration, ash-free dry mass of benthic organics, and algal composition were determined from five cobbles removed from upper littoral zone (approximately 0.25 m depths) following the methods of Lebkuecher et al. (2015). Phytoplankton richness was estimated from multiple samples collected with phytoplankton nets (120-µm pore size) and Van Dorn samplers. Phytoplankton were preserved in 1 % glutaraldyde and concentrated by settling in darkness. Algae were identified to the lowest taxon possible using references listed in Grimmett and Lebkuecher (2017). Indices including the algae trophic index of soft algae assemblages (ATI, Grimmett and Lebkuecher 2017) and the pollution tolerance index for diatom assemblages (PTI, KDOW 2008) were used to infer the impact of trophic status on benthic algal assemblages. The ATI was calculated as: ATI = [$\Sigma_{j = 1\ taxon}$ n_j ti_j]/N where: n_j = number of taxon units j sampled at a site, ti_j = trophic-indicator value for taxon j, and N = total number of taxon units at the sampling site used to calculate the index (Grimmett and Lebkuecher 2017). The trophic-indicator values are the abundance-weighted averages of benthic [chl *a*] listed in Grimmett and Lebkuecher (2017). The pollution tolerance index for diatom assemblages (PTI; KDOW 2008) was calculated as: PTI = [$\Sigma_{j=1\ sp.}$ n_j t_j]/N where: n_j = number of individuals of

taxon j, t_j = eutrophication-tolerance value for taxon j, and N = total number of individuals assigned a eutrophication-tolerance value and tallied to calculate the index. The eutrophication-tolerance values range from one (taxon very tolerant to eutrophic conditions) to four (taxon very intolerant to eutrophic conditions) and are based on decades of autecological studies (KDOW 2008). Although trophic indicator values assigned to taxa for both the ATI and PTI were determined from evaluations of streams and rivers, these indices were used because indices specific to lotic environments have yet to be developed.

Results and discussion

The physical characteristics of Swan Lake (Table 1) are typical of lentic environments in Tennessee. For example, the slightly basic pH is similar to other aquatic systems in the ecoregion given the limestone geologic base. The relatively low n" of Swann Lake on 9 Sept. 2019 most likely reflects the lack of significant precipitation, thus lack of sediment runoff during the previous two weeks. The majority of the light-extinction studies from a variety of natural freshwater lakes and reservoirs with different morphologies and chemistries report n" values near 1.3, a value which has been adopted as typical for purposes of comparison (Renolds 1990). Values of n" $\geq$ 1.8 indicate unusually high concentrations of suspended matter (Luettich et al. 1990). The relatively low concentration of suspended particles in Swan Lake is verified by the low value for the nephelometric turbidity units (NTU). For example, NTU values above 25 indicate the water column contains an unhealthy concentration of suspended particles (USEPA 1986).

Table 1. Physical characteristics of Swan Lake on Sept. 9, 2019.

pH at 0.25 m at 9:30 AM CST	7.1
Light extinction coefficient (n")	1.0 ± 0.1
Nephelometric turbidity units	21 ± 5
Total phosphorus ($\mu g \cdot L^{-1}$)	20
Total nitrogen ($\mu g \cdot L^{-1}$)	841
Total phosphorus to total nitrogen ratio	42

The concentration of total phosphorus (TP) of water collected from Swan Lake is in the range suggested by Carlson and Simpson (1996) to designate lakes as mesotrophic (> 12 μg TP $\cdot L^{-1}$ to < 25 μg TP $\cdot L^{-1}$). The high ratio of total nitrogen (TN) to TP suggests P limits photoautotroph growth in Swan Lake. For example, P may be considered limiting when the TN:TP ratio by mass is > 33 (Carlson & Simpson 1996). The ratio of TN to TP of Swann Lake was expected given P limits algae biomass in most freshwaters. The concentration of P is a primary criterion used to designate trophic status of aquatic habitats although several studies have demonstrated that eutrophic environments with high concentrations of algae may have low water [P] as a result of high P demand (Grimmett & Lebkuecher 2017).

The low concentration of chl *a* of the water column of Swan Lake (Table 2) indicates that the productivity of the water column was relatively low. For example, concentrations of water column chl *a* > 7.3 µg/L are indicative of eutrophic conditions (Carlson & Simpson 1996). The rates of photoautotrophic periphyton production (Table 2) are substantially lower than rates considered typical of eutrophic environments and support the conclusions from analyses of the concentration of chl *a* of the water column that the productivity of the water column is low. For example, primary production values $\leq$ 0.3 mg chl *a* $\cdot m^{-2} \cdot day^{1}$ are typical of aquatic environments with good quality water in Middle Tennessee (Lebkuecher et al. 2009).

The mean value for the biochemical oxygen demand 5-day assay (BOD_5 assay) is typical for those determined from samples without excessive concentrations of organics. BOD_5 values from water without excessive concentrations of organics range from near 0 to 8 mg O_2 consumed $\cdot L^{-1} \cdot 5\ d^{-1}$, while values of wastewater from wastewater treatment plants are often above 19 mg O_2 consumed $\cdot L^{-1} \cdot 5\ d^{-1}$ (Delzer & McKenzie 2003; Yun & An 2016).

Table 2. Biomass characteristics, OD_{664} to OD_{665} ratio, and biochemical oxygen demand (means $\pm$ S.E.) of Swan Lake.

Water column chlorophyll *a* ($\mu g \cdot L^{-1}$)	4.3 ± 0.2
Primary production on artificial substrates (mg chlorophyll *a* $\cdot m^{-2} \cdot day^{-1}$)	0.1 ± 0.0
Biochemical oxygen demand (mg $0_2 \cdot L^{-1} \cdot 5\ days^{-1}$)	2.6 ± 0.3
Benthic (cobble) chlorophyll *a* ($mg \cdot m^{-2}$)	91.2 ± 29.1
OD_{664} to OD_{665} ratio	1.6 ± 0.02
Ash-free dry mass of benthic organics ($g \cdot m^{-2}$)	12.1 ± 3.0

Concentrations of benthic chl *a* were > 70 $mg \cdot m^{-2}$, a value suggested by Dodds et al. (1998) to designate aquatic systems as eutrophic. The OD_{664} to OD_{665} ratio of pigment extracts indicate the photoautotrophic periphyton collected from Swan Lake were in good physiological condition. Because pigment extracts from healthy algae may have no detectable pheophytin *a* determined by optical density (OD) measurements using a spectrophotometer, the chl *a* to pheophytin *a* ratio is indicated as the ratio of OD_{664} to OD_{665}. Pheophytin *a* is a chl *a* degradation product. An OD_{664} to OD_{665} ratio of 1.7 is interpreted as no detectable pheophytin *a* present and ratios < 1.5 indicate the algae contained high concentrations of pheophytin *a* (Baird et al. 2017).

The concentrations of ash-free dry mass of benthic organic matter was > 10 $g \cdot m^{-2}$, a value indicative of eutrophic environments (O'Brian & Wehr 2010). This result supports the conclusions from the measurements of the concentrations of benthic chl *a* that demonstrate an unhealthy concentration of benthic photoautotrophic periphyton biomass. The high concentrations of benthic chl *a* and ash-free dry mass of benthic organic matter indicate that periphyton characteristics of Swan Lake are a more accurate indicator of the lake's eutrophic status relative to water-column characteristics measured such as nutrient concentration of water, chl *a* concentration of water, and primary production rate on artificial substrates suspended in the water column.

We identified 69 taxa of soft algae (Appendix 1). The most abundant benthic soft alga sampled was the filamentous cyanobacterium *Leptolyngbya angustissimum* (West & West) Anagn. & Komárek (28.1 %) followed by *Oedogonium* sp. (12.0 %) and *Cladophora glomerata* (L.) Kütz. (10.9 %). The taxa richness of the benthic soft-algal assemblage was lower relative to the phytoplankton assemblage (Table 3). The low Shannon diversity index for the benthic soft-algal assemblage in Swan Lake is typical for soft algal assemblages in Middle Tennessee (Lebkuecher et al. 2018b) is due largely to the low evenness value. The high value for the algae trophic index (ATI) for the benthic soft algal assemblage indicates this assemblage is impacted by eutrophication. ATI values correspond with Dodds et al. (1998) suggested classification of [benthic chl *a*] $\geq$ 70 $mg \cdot m^{-2}$ as eutrophic. The high value for the ATI is due partially to the high abundance of *Cladophora glomerata* (L.) Kütz. (10.9 %) which has a high trophic-indicator value used to calculate the ATI given *C. glomerata* is common at eutrophic sites (Grimmett & Lebkuecher 2017).

We identified 38 taxa of benthic diatoms (Appendix 2). The most abundant diatom sampled was *Achnanthidium minutissimum* (Kütz.) Czarn. (28.1 %) followed by *Achnanthidium* sp. (9.6 %), and *Cocconeis placentula* Ehrenb. (7.9 %). The higher value for the Shannon diversity index for the diatom assemblage (Table 4) relative to the soft algal assemblage (Table 3) is due largely to the greater

evenness value for the diatom assemblage. Greater values for evenness and the Shannon diversity index of diatom assemblages relative to soft algal assemblages are typical of benthic communities in Middle Tennessee (Lebkuecher et al. 2018b). The low value for pollution tolerance index (PTI) for the diatom assemblage indicates the assemblage is impaired by nutrient enrichment. A value for the PTI < 2.6 is a suggested value to indicate an assemblage is substantially impacted by eutrophic conditions (Lebkuecher et al. 2018b). The low PTI value for the diatom assemblage in Swan Lake results largely from the high percent compositions of *Navicula* and *Nitzschia* taxa, most of which are assigned low trophic-indicator values for the PTI given they are typically more abundant in eutrophic habitats (KDOW 2008).

Table 3. Metrics and indices for the benthic soft-algal assemblage and phytoplankton richness of Swan Lake.

Index	Index value
Taxa richness of benthic soft algae	41
Taxa richness of phytoplankton	49
Shannon diversity index for benthic soft algae	2.3
Evenness for benthic soft algae	0.6
Algae trophic index for benthic soft algae	77

Table 4. Metrics and indices of the benthic diatom assemblage sampled from cobbles in Swan Lake.

Index	Index value
Taxa richness	41
Shannon diversity index	2.8
Evenness	0.7
Pollution tolerance index	2.6

Conclusions

Concentrations of total phosphorus and total nitrogen of water sampled from Swan Lake were below those expected in a eutrophic environment, most likely due to high demand. Other water-column characteristics including chl *a* concentration, biochemical oxygen demand, and primary production on suspended substrates were also below levels expected in a eutrophic environment and likely reflect the low concentration of water-column nutrients. Periphyton characteristics including a high concentration of chl *a*, high concentration of ash-free dry mass of benthic organics, and values for algal indices of the benthic assemblages accurately indicate the trophic status of Swan Lake. The results indicate that periphyton characteristics best characterize the trophic status of Swan Lake relative to water-column characteristics and that assessment and monitoring of eutrophic lentic habitats should include measurements of periphyton characteristics.

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Appendix 1. Percent composition of benthic soft-algal taxa sampled from cobbles, benthic soft-algal taxa sampled from cobbles present (P) observed independently of determinations of percent composition, and phytoplankton taxa present (P) sampled from the water column in Swan Lake listed in alphabetical order by phylum.

Chlorophyta	**Percent composition of benthic soft-algal taxa**	**Phytoplankton taxa present (P)**
Aphanochaete polychaete (Hansg.) Fritsch.		P
Bulbochaete sp.	0.71	P
Chlamydomonas patellaria Whitford		P
Chlamydomona gloeogama Korshikov		P
Chlamydomonas sp.	0.02	
Chlorococcum humicola (Nägeli) Rabenh.	0.04	
Cladophora glomerata (L.) Kütz.	10.91	
Coelastrum microporum Nägeli	0.36	P
Coelastrum reticulatum (Dang.)		P
Cosmarium botrytis Menegh.	0.69	P
Cosmarium contractum Kirchn.		P
Cosmarium galeritium Nordst.	3.28	P
Cosmarium raciborskii (Racib.) Lagerh.	4.028	
Cosmarium sp.	0.02	P
Cosmarium subprotumidum Nordst.	0.09	P
Cosmarium turpinii Bréb.	0.07	P
Desmidium sp.		P
Gloeocystis gigas (Kütz.) Langerh.	3.74	P
Gloeocystis vesiculosa Nägeli	10.49	P
Mougeotia sp.	10.08	P
Oedogonium sp.	11.99	P
Oocystis sp.		P
Pandorina morum (Müller) Bory	0.47	P
Pediastrum araneosum (Racib.) G. M. Sm.	0.17	
Pediastrum integrum (Meyen 1829)		P
Pediastrum sp.	0.37	P

Pediastrum tetras (Ehrenb.)		P
Scenedesmus acuminatus (Lagerh.) Chodat	0.06	
Scenedesmus bijuga (Turp.) Lagerh.	0.51	P
Scenedesmus dimorphus (Turp.) Kütz.	0.04	
*Scenedesmus obliquus (*Turp.) Kütz.		P
Scenedesmus quadricauda (Turp.) Bréb.	0.07	
Scenedesmus sp.	0.06	
Selenastrum capricornutum Printz	0.06	P
Spirogyra sp.		P
Staurastrum obliculare (Erenb.) Ralfs	0.02	P
Staurastrum sp.		P
Sphaerocystis sp.		P
Sphaerocystis planktonia (Korsh.) Bourr.	0.34	
Volvox globulator (L.)		P
Zygnema sp.		P
Cyanobacteria		
Aphanocapsa elachista West and West		P
Chroococcus minor (Kütz.) Nägeli	0.04	
Chroococcus minutus Kütz.		P
Chroococcus sp.		P
Coelosphaerium sp.	0.21	
Dactylococcopsis raphidiodes (Hansg.) Chodat and Chodat		P
Komvophoron munitum (Skuja) Anagn. and Komárek		P
Leibleinia nordgaardii (Wille) Anagn. and Komárek	0.66	P
Leptolyngbya angustissimum (West and West) Anagn. and Komárek	28.11	P
Leptolyngbya sp.	4.68	P
Merispodedia tenuissima Lemmerm.	P	
Microcystis aeruginosa (Kütz.) Kütz.	0.02	
Microcystis incerta Lemmerm.	0.02	
Oscillatoria agardhii Gomont	0.09	
Oscillatoria limosa (Dylwin) C. Agardh		P
Oscillatoria sp.	0.24	P
Oscillatoria subtilissima Kütz. and De Toni	2.44	
Phormidium articulatum (Gardner) Anagn. and Komárek	0.37	
Phormidium diguetii (Gomont) Anagn. and Komárek	0.32	
Phormidium sp.	7.49	P
Synechocystis sp.	0.02	
Dinophyta		
Peridinium sp.		P
Euglenophyta		
Euglena sp.		P
Cryptophyta		
Chroomonas nordstedtii Hansg.		P

Chrooomonas sp.		P
Cryptomonas erosa Erenb.		P
Ochrophyta		
Dinobryon sp.		P
Lagynoin sp.	P	

Appendix 2. Percent composition of benthic diatom taxa sampled from cobbles and benthic diatom taxa sampled from cobbles present (P) observed independently of determinations of percent composition in Swan Lake listed in alphabetical order.

Taxon name	Percent composition
Achnanthidium gracillimum Lange-Bert.	2.31
Achnanthidium minutissimum (Kütz.) Czarn.	28.05
Achnanthidium rivulare Potapova and Ponander	5.28
Achnanthidium sp.	9.57
Cocconeis placentula Ehrenb.	7.92
Cocconeis placentula var. euglypta Ehrenb.	0.33
Cymatopleura solea (Bréb. and Godey) W. Sm.	0.33
Eunotia pectinalus (Kütz.) Rabenh.	P
Eunotia sp.	0.99
Frustulia vulgaris (Thwaites) De Toni	0.33
Gomphoneis olivacea (Horn.) Daws.	0.33
Gomphonema acutinatum Ehrenb.	0.66
Gomphonema angustatum (Kütz.) Rabenh	1.98
Gomphonema gracile Ehrenb.	0.33
Gomphonema minutum Ag.	0.66
Gomphonema parvulum (Kütz.) Kütz.	0.33
Gomphonema pseudoaugur Lange-Bert.	0.33
Gomphonema truncatum Ehrenb.	0.33
Melosira varians Ag.	6.60
Navicula capitatoradiata Germ.	4.62
Navicula cryptocephala Kutz.	1.65
Navicula crytotenella Lange-Bert.	P
Navicula lanceolata (Ag.) Ehrenb.	0.33
Navicula menisculus var. *upsaliensis* (Grun.) Grun.	0.66
Navicula sp.	1.98
Navicula veneta Kütz.	1.98
Nitzschia acicularis (Kütz.) W. Sm.	0.66
Nitzchia amphibia Grun.	1.65
Nitzschia angustata (W. Sm.) Grun.	0.33
Nitzschia capitellata Hust.	2.64
Nitzschia fonticola Grun.	0.66
Nitzschia frustulum (Kütz.) Grun.	1.65
Nitzschia inconspicua Grun.	1.32
Nitzschia sinuata var. tabellaria Grun.	0.66
Nitzschia flexa Schumann	P
Nitzschia sociabilis Hust.	1.98
Synedra delicatissima W. Sm.	2.31

Thalassiosira weissflogii (Grun.) G. Fryxell and Hasle	0.33
Ulnaria sp.	0.66
Ulnaria ulna (Nitzsch.) Compère	0.66
Ulnaria capitata (Erenb.) Compère	6.60

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FIRST RECORD OF *CASTILLEJA PECKIANA* (OROBANCHACEAE) FOR CALIFORNIA

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ABSTRACT

A recent collection of *Castilleja peckiana* Pennell from Modoc County, California, is documented and illustrated. While the species is known from the directly adjacent Lake Co., Oregon, this collection represents the first verified occurrence for this species in the state of California.

Castilleja peckiana Pennell is an uncommon species of moderate elevations (1000-2600 m) in sagebrush-juniper associations and open ponderosa pine or Douglas-fir communities, primarily in eastern Oregon (Baker, Crook, Deschutes, Grant, Harney, Lake, Malheur, Morrow, Union, Wallowa, and Wheeler cos.), as well as in northern Elko Co., Nevada (Holmgren 1984), and more recently documented occurrences in Adams and Owyhee counties in Idaho (Egger et al. 2019). While documented populations of *C. peckiana* approach the California border in the vicinity of Summer Lake in adjacent Lake Co., Oregon, about 95 kilometers north of the border (Oregon Plant Atlas 2020, IRHN 2020), there are no previous records of its presence in California (Wetherwax et al. 2012, 2020; CCH1 2020; CCH2 2020).

California. Modoc Co.: Modoc Plateau, Devil's Garden area, along Road 47N99 along the SE side of Bird Spring Ridge, 5.1 air-km NW of Blue Mountain, T47N, R9E, SW¼ of SW¼ of sec. 36, Pothole Valley 7.5' quad; 41.869444, -120.891111 WGS84, 1544 m, 11 Jun 2018, *Janeway 12627* (CHSC, WTU). Figures 1, 2.

This population is located about 15 kilometers south of the Oregon border and about 110 kilometers south of the nearest known populations and represents the first verified occurrence for this species in the state of California.

The collection documented here was originally identified as *Castilleja chromosa* A. Nels., but that species can be distinguished from *C. peckiana* with the following couplet.

1. Stems usually 1.5-3.5 dm tall, rarely branched above, with conspicuous, hispid pubescence; leaves with 0-3 pairs of lateral lobes; bracts with 1–3 pairs of lateral lobes with +/- rounded apices ..... **Castilleja chromosa**
1. Stems 3-5 dm tall, often branched above, with relatively inconspicuous, +/- cinerous puberulence; leaves with 0-1 pair of lateral lobes; bracts with 1(–2) pairs of lateral lobes with +/- acute apices ..... **Castilleja peckiana**

Images of the holotype of *Castilleja peckiana* (Fig. 3) and of typical plants in the field (Figs. 4-6) are presented below.

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Figure 1. *Castilleja peckiana*, Devil's Garden area, Modoc Plateau, Modoc Co., California, 11 June 2018, *Janeway 12627*, CHSC.

Figure 2. *Castilleja peckiana*, Devil's Garden area, Modoc Plateau, Modoc Co., California, 11 June 2018, *Janeway 12627*, CHSC. Details of two inflorescences and lower stem.

Figure 3. Holotype of *Castilleja peckiana*, Deschutes Co., Oregon, *F.W. Pennell 15503* (PH).

Figure 4. *Castilleja peckiana*, 6-7 mi SE of Page Springs along Steens Mountain Loop Road, Harney County, Oregon, 10 Jul 1994, *Egger 651* (WTU). Photo by J.M. Egger.

Figure 5. *Castilleja peckiana*, Steens Mountain Loop Road below Fish Lake, Harney Co., Oregon, 10 July 1994 (no collection). Photo by J.M. Egger.

Figure 6. *Castilleja peckiana*, ca. 13 mi. SE of Page Springs along Steens Mountain Loop Road, Harney Co., Oregon, 1 July 1985, *Egger 131* (WTU). Photo by J.M. Egger.

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STIPITATE AND NON-STIPITATE FORMS OF *ERICAMERIA GREENEI* (ASTERACEAE)

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ABSTRACT

Leaves of typical *Ericameria greenei* have sunken glands, while those in the northeastern part of the range (central Idaho, northeastern Oregon and northern Washington) have raised, stipitate glands. The two forms are distinctly allopatric in Idaho and Washington, dividing the overall distribution of *E. greenei* into two segments, but stipitate-glandular forms occur sporadically, probably as populational variants, in the range of the non-stipitate populations (typical *E. greenei*). Two taxa might be formally recognized among the *E. greenei* populations, but a principal components analysis indicates that both gland forms are reasonably included within the single species, distinguishable from the closely related *E. bloomeri*, which is consistently non-stipitate. The presence of stipitate glands is an unreliable character to distinguish *E. greenei* from *E. bloomeri*. *E. bloomeri* does not occur in Idaho.

Ericameria greenei (A. Gray) Nesom and *Ericameria bloomeri* (A. Gray) J.F. Macbr. are small shrubs in Asteraceae with several to many heads per branch. Most authors now treat *E. greenei* and *E. bloomeri* as separate species (Urbatsch 2012; Legler et al. 2018; Urbatsch et al. 2006; Jaster et al. 2017), but the two are morphologically similar, both placed in sect. *Macronema* (Hall 1928; Nesom 1990). Both are positioned within the same clade by analysis of nuclear ribosomal 3' ETS and ITS sequences (Roberts & Urbatsch 2003). *Ericameria suffruticosa* (Nutt.) Nesom is the only species more closely related to *E. greenei* than *E. bloomeri* (Roberts & Urbatsch 2003).

Different sources distinguish *Ericameria greenei* and *E. bloomeri* using different characters. Urbatsch et al. (2006) differentiate *E. greenei* from *E. bloomeri* by the presence or absence of stipitate glands on their leaves, claiming that *E. greenei* possesses stipitate glands (Figure 2) and *E. bloomeri* non-stipitate, resinous glands (Figure 3). Hall (1928), however, noted that foliage of *E. greenei* has glands that are "minutely stalked in rare cases." Furthermore, the lectotype of Greene's collection of *E. greenei* from northern California lacks stipitate glands (Nesom, personal communication) as do all collections of *E. bloomeri*. Cronquist (1994) considered *E. greenei* as a variety of *Haplopappus bloomeri* A. Gray—*H. bloomeri* var. *greenei* (A. Gray) Cronquist. Cronquist noted that "both varieties embrace glandular and tomentose-puberulent phases that often grow intermingled." Legler et al. (2018) recognize *E. greenei* first by its shorter, wider, and more oblanceolate or spatulate leaves—compared to *E. bloomeri*'s longer, narrower, and more filiform to linear-oblong leaves—secondly by less pronounced difference in outer and inner phyllary length, and lastly in its more compact inflorescence.

The confusion surrounding the relationship of glandularity to other morphological characters in *Ericameria greenei* and *E. bloomeri* led to our study. Our recent collections of *Ericameria* from the Owyhee Mountains of southern Idaho consistently lack stipitate glands (Figure 1) placing them with the type of *E. greenei*, while collections elsewhere in Idaho consistently possess stipitate glands. Ambiguity in current floristic treatments result in different interpretations of specimens from the Owyhee Mountains and Idaho north of the Snake River Plain. Furthermore, in lacking stipitate glands it seemed plausible that Owyhee Mountains specimens may best be classified as *E. bloomeri* despite having wider and shorter leaf dimensions that would otherwise place them in *E. greenei*. If they are to be classified as *E. greenei*, then should there be varietal distinction between the non-stipitate forms in

the Owyhee Mountains and those with stipitate glands in the rest of Idaho north of the Snake River? This study investigates the taxonomy of plants identified as *E. greenei* using the criteria of Legler et al. (2018), which include both stipitate and non-stipitate forms. Our goal is to understand the morphological relationship of glandular characteristics to other morphological characters in both *E. greenei* and *E. bloomeri* in relationship to their geographic ranges, and to determine the identities of Idaho plants.

Specimens of *Ericameria suffruticosa* were also examined in our preliminary investigations. These plants have wider and oblanceolate leaves similar to *E. greenei* (Legler et al. 2018; Urbatsch et al. 2006; Urbatsch 2012). But unlike *E. greenei*, *E. bloomeri*, and the Owyhee collections, *E. suffruticosa* has fewer heads (1–3 per branch), more flowers per head, and even more pronounced glandular stipes (Urbatsch et al. 2006; Legler et al. 2018; Hall 1928). Based on these criteria and our preliminary results, we chose not to include *E. suffruticosa* in our study despite its obvious close relationship to the other two species. *Ericameria suffruticosa* has never been found in the Owyhee Mountains.

Understanding the taxonomy of the Owyhee Mountains plants has implications for their conservation status. If treated as *E. bloomeri,* these plants would represent a significant range extension for that species and also be the only populations of *E. bloomeri* in Idaho. If all Idaho populations are treated as *E. greenei,* then *E. bloomeri* would otherwise be absent from Idaho. Alternatively, if significant morphological and coherent geographic variation exists among stipitate and non-stipitate populations of *E. greenei,* then regarding the two as separate taxa might be justified.

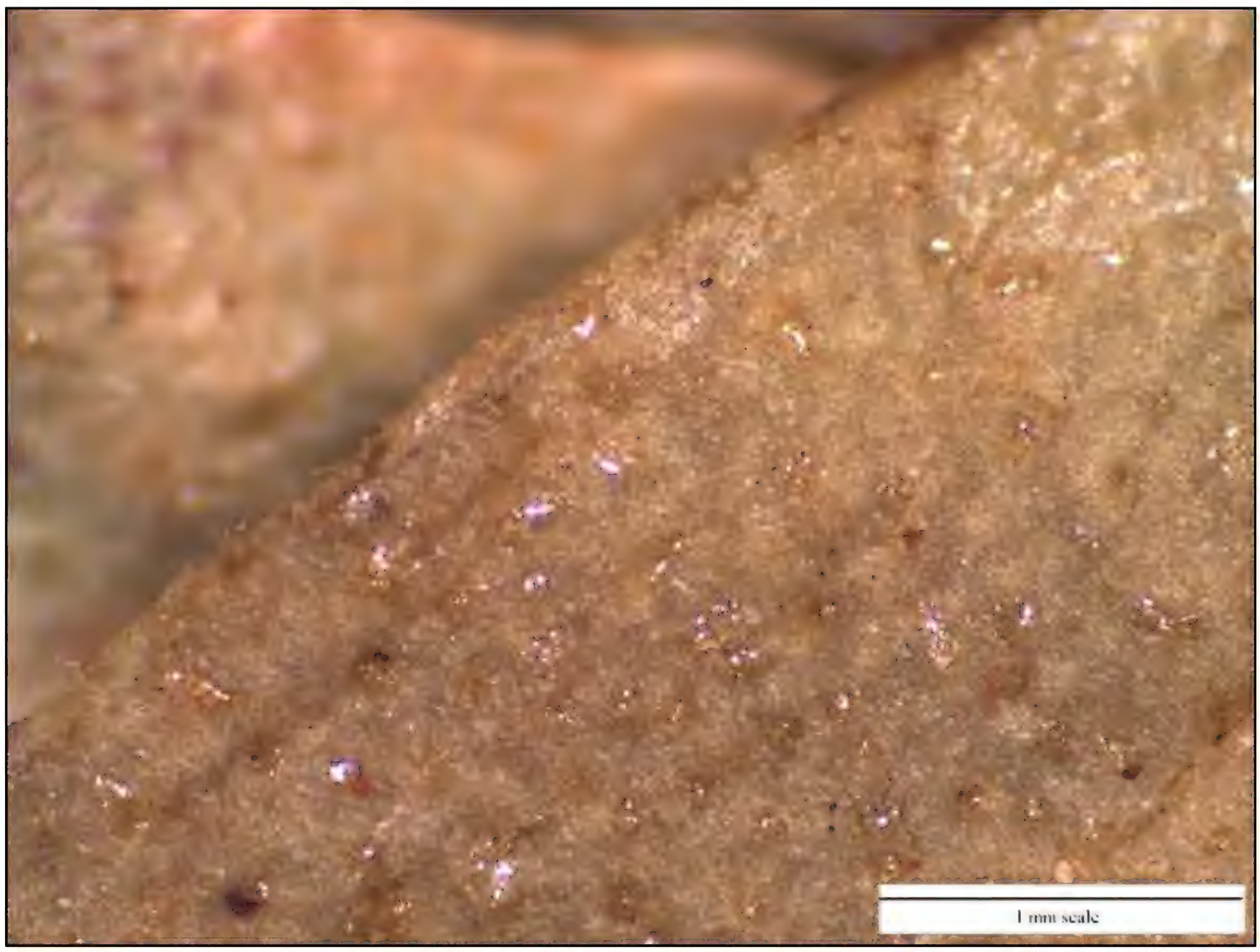

Figure 1. Non-stipitate *Ericameria greenei* from Owyhee Mountains of southern Idaho. Glands are present as "resin dots" in shallow pits at the leaf surface. Compare *E. bloomeri* in Figure 3.

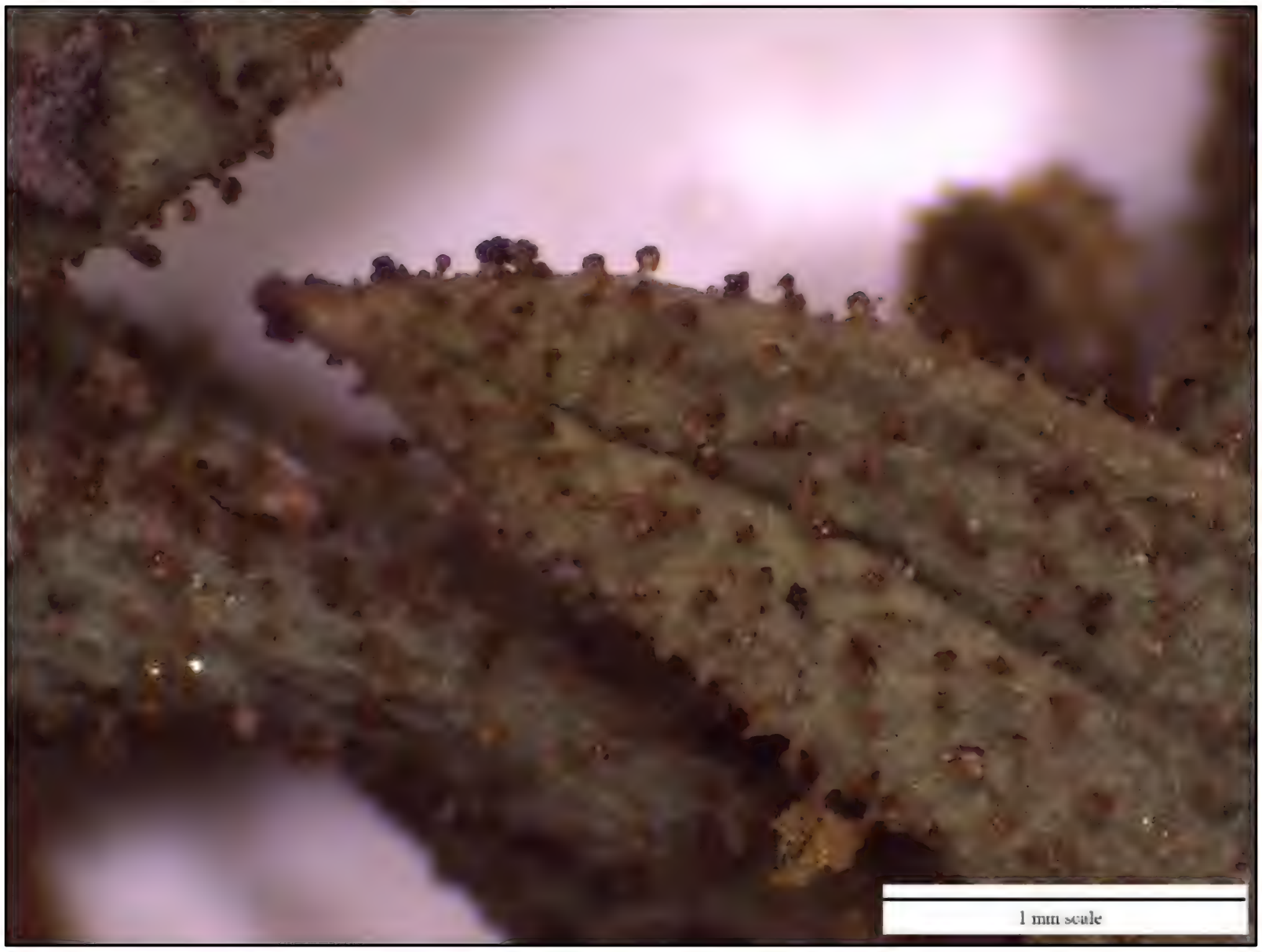

Figure 2. *Ericameria greenei* leaf with stipitate-glands, typical of northern Idaho collections.

Figure 3. *Ericameria bloomeri* — leaf glands ("resin dots") lack stipes.

Methods

We examined all specimens of *Ericameria bloomeri* and *E. greenei* identified as such using the criteria of Legler et al. (2018) from The College of Idaho (CIC), Boise State University (SRP), University of Nevada (RENO), Washington State University (WTU), and Oregon State University (OSC, WILLU). We then selected 130 specimens representing the full range of morphologic and geographic variation described in literature (Table 1; Urbatsch 2012; Legler et al. 2018; Urbatsch et al. 2006; Jaster et al. 2017). We measured the 24 characters listed in Table 2 on these specimens and performed a One Way ANOVA on a subset of 62 specimens. Using the 16 characters found to be significant (Table 2), we performed a Principal Components Analysis (PCA) on a subset of 93 specimens chosen to include all non-stipitate forms of *E. greenei* from the Owyhee Mountains, 22 non-stipitate *E. greenei* from elsewhere, 31 stipitate forms of *E. greenei,* and 31 specimens of *E. bloomeri*. Sigma Plot 3.0 was used for all statistical analyses. We created a map of the geographic range of the 130 specimens selected based on the latitude and longitude noted by the collector. If a Public Land Survey System township and range was given instead, we converted it to latitude and longitude using Earth Point <http://www.earthpoint.us/Townships.aspx>. If only the name of a location was given, Google Earth Pro 2019 was used to georeference that location. The latitude and longitude data were compiled and the website Copy Paste Map < http://copypastemap.com/> was used to produce a map from the data.

Table 1. Specimens used in this study. Stipitate forms of *E. greenei* are referred to as *E. greenei*.

Accession #	State	County	Latitude, Longitude	Collector	Coll. #	Taxon	Included in
CIC 044862	ID	Owyhee	43.0047, -115.7003	C. Davidson	12106	Nonstip. E. greenei	ANOVA, PCA
CIC 045731	CA	Plumas	40.06, -121.24	B. Corbin	1535	E. bloomeri	ANOVA, PCA
CIC 018526	ID	Valley	45.14, -115.92	L. Smithman	895	E. greenei	ANOVA, PCA
CIC 023469	OR	Harney	42.71, -118.63	D. Mansfield	90-586	E. greenei	ANOVA, PCA
CIC 017844	ID	Idaho	43.76, -114.31	B. Ertter	3996	E. suffruticosa	ANOVA, PCA
CIC 050434	ID	Owyhee	43.00211, -116.70383	D. Mansfield	15-374	Nonstip. E. greenei	ANOVA, PCA
CIC 038738	ID	Lemhi	45.12, -114.60	B. Ertter	9511	E. greenei	ANOVA, PCA
CIC 024062	OR	Harney	42.63, -118.59	D. Mansfield	92-206	E. greenei	ANOVA, PCA
CIC 037070	ID	Owyhee	42.9862, -116.6922	D. Mansfield	9407	Nonstip. E. greenei	ANOVA, PCA
CIC 025875	ID	Owyhee	43.0609, -116.8579	A. DeBolt	1523	Nonstip. E. greenei	ANOVA, PCA
CIC 044027	ID	Owyhee	42.67063, -116.43857	E. George	445	Nonstip. E. greenei	ANOVA, PCA
CIC 019416	ID	Owyhee	42.6849, -116.7943	R. Rosentrater	3252	Nonstip. E. greenei	ANOVA, PCA
CIC 016288	ID	Owyhee	42.9511, -116.6357	W. Baker	8198	Nonstip. E. greenei	ANOVA, PCA
CIC 050436	ID	Owyhee	42.97638, -116.71542	D. Mansfield	15-379	Nonstip. E. greenei	ANOVA, PCA
CIC 021002	ID	Owyhee	43.0173, -116.7785	L. Smithman	1970	Nonstip. E. greenei	ANOVA, PCA
CIC 017695	ID	Idaho	45.26, -116.14	L. Smithman	537	E. greenei	ANOVA, PCA
CIC 017975	ID	Adams	45.10, -116.20	N. Tobias	sn	E. greenei	ANOVA, PCA
CIC 044632	ID	Idaho	45.225, -115.977	B. Ertter	21200	E. greenei	ANOVA, PCA
CIC 020914	ID	Valley	44.95, -115.96	L. Smithman	776	E. greenei	ANOVA, PCA
CIC 016287	ID	Boise	43.97, -114.99	P. Packard	73-226	E. greenei	ANOVA, PCA
CIC 016285	ID	Custer	44.00, -114.95	P. Packard	73-254	E. greenei	ANOVA, PCA
CIC 051057	ID	Elmore	43.61172, -115.42118	D. Mansfield	16393	E. greenei	ANOVA, PCA
CIC 052520	ID	Custer	43.814645, -114.13373	D. Mansfield	17382	E. greenei	ANOVA, PCA
CIC 013273	ID	Valley	45.03, -115.92	L. Smithman	439	E. greenei	ANOVA, PCA
CIC 022923	ID	Valley	44.39, -115.53	H. Clouser	91-150	E. greenei	ANOVA, PCA
CIC 002995	ID	Valley	44.85, -115.95	B. Ertter	7405	E. greenei	ANOVA, PCA
CIC 020924	ID	Valley	45.01, -115.88	L. Smithman	737	E. greenei	ANOVA, PCA
CIC 013276	ID	Valley	45.09, -115.90	L. Smithman	453	E. greenei	ANOVA, PCA
CIC 016286	ID	Valley	44.99, -116.11	B. Ertter	422/2	E. greenei	ANOVA, PCA

Accession #	State	County	Latitude, Longitude	Collector	Coll. #	Taxon	Included in
CIC 002994	ID	Adams	45.09, -116.21	B. Ertter	7347	E. greenei	ANOVA, PCA
CIC 027197	ID	Valley	44.42, -116.14	C. Baun	20	E. greenei	ANOVA, PCA
CIC 017693	ID	Idaho	45.25, -116.15	L. Smithman	539	E. greenei	ANOVA, PCA
CIC 020924	ID	Idaho	45.22, -115.98	L. Smithman	767	E. greenei	ANOVA, PCA
CIC 045832	ID	Idaho	45.246, -116.132	B. Ertter	21606	E. greenei	ANOVA, PCA
CIC 024959	ID	Harney	42.75, -118.60	H. Sheldon	11	E. greenei	ANOVA, PCA
CIC 28812	ID	Clearwater	46.52, -116.30	J. Duft	1345	E. greenei	ANOVA, PCA
CIC 045827	ID	Idaho	45.246, -116.132	B. Ertter	21607	E. greenei	ANOVA, PCA
CIC 27610	ID	Boise	44.00, -115.34	J. Duft	58	E. greenei	ANOVA, PCA
CIC 036675	ID	Valley	44.56, -116.18	B. Ertter	9593	E. greenei	ANOVA, PCA
CIC 036676	ID	Valley	44.56, -116.18	B. Ertter	9592	E. greenei	ANOVA, PCA
CIC 025468	OR	Harney	42.63, -118.58	D. Mansfield	94-47	E. greenei	ANOVA, PCA
CIC 023471	OR	Harney	42.71, -118.57	D. Mansfield	90-450	E. greenei	ANOVA, PCA
RENO 37395	NV	Ormsby	39.15, -119.88	A. Tiehm	2840	E. bloomeri	ANOVA, PCA
RENO 32050	NV	Washoe	39.59, -119.93	M. Williams	72-70-4	E. bloomeri	ANOVA, PCA
RENO 29709	NV	Washoe	39.95, -119.80	R. Evans	sn	E. bloomeri	ANOVA, PCA
RENO 11105	CA	Alpine	38.69, -119.83	C. Saulisberry	31	E. bloomeri	ANOVA, PCA
RENO 62107	CA	Modoc	41.80, -120.21	M. Williams	83-154-1	E. bloomeri	ANOVA, PCA
RENO 59125	CA	Siskiyou	41.58, -121.58	M. Williams	85-69-1	E. bloomeri	ANOVA, PCA
RENO 52926	CA	El Dorado	38.8697, -120.0297	E. Dean	4490	E. bloomeri	ANOVA, PCA
RENO 11353	NV	Washoe	39.59, -119.93	W. Billings	1454	E. bloomeri	ANOVA, PCA
SRP 27898	ID	Klamath	38.0856, -121.9517	R. Halse	6676	E. bloomeri	ANOVA, PCA
SRP 051496	CA	Plumas	39.99, -121.24	F. Oswald	8876	E. bloomeri	ANOVA, PCA
SRP 018278	OR	Deschutes	43.96, -121.22	R. Halse	2747	E. bloomeri	ANOVA, PCA
RENO 53012	OR	Jackson	42.08, -122.72	S. Sundberg	2638	Nonstip. E. greenei	PCA
SRP 018274	OR	Josephine	42.09, -123.36	W. Baker	638	Nonstip. E. greenei	PCA
SRP 018273	OR	Wallowa	45.24, -117.29	G. Mason	1713	Nonstip. E. greenei	PCA
SRP 018272	OR	Klamath	43.16, -121.78	J. Leiberg	sn	Nonstip. E. greenei	PCA
SRP 023967	OR	Linn	44.41, -121.88	M. Thompson	95121	Nonstip. E. greenei	PCA
OSC 32846	OR	Hood River	45.37, -121.70	H. Gilkey	sn	Nonstip. E. greenei	PCA
OSC 178811	OR	Douglas	43.15, -122.45	J. Fosback	699	Nonstip. E. greenei	PCA
ORE 107517	OR	Linn	44.46, -121.90	J. Hickman	497-3	Nonstip. E. greenei	PCA
OSC 22191	OR	Klamath	43.03, -122.12	R. Pendleton	sn	Nonstip. E. greenei	PCA
OSC 35873	OR	Klamath	42.90, -122.08	Scullen	sn	Nonstip. E. greenei	PCA
OSC 31531	OR	Lake	43.13, -120.16	E. Anderson	sn	Nonstip. E. greenei	PCA
OSC 130583	OR	Lane	44.10, -121.77	G. Vecten	58-221	Nonstip. E. greenei	PCA
OSC 11955	OR	Siskiyou	41.41, -122.19	A. Heller	14438	Nonstip. E. greenei	PCA
OSC 73699	OR	Harney	42.64, -118.58	K. Dahle	122	Nonstip. E. greenei	PCA
ORE 09191	NV	Clark	35.97, -114.77	I. Clokey	8570	Nonstip. E. greenei	PCA
RENO 52909	NV	Washoe	39.59, -119.93	M. Williams	7185	Nonstip. E. greenei	PCA
ORE 94123	NV	Lake	42.22, -120.10	D. Yiagst	sn	Nonstip. E. greenei	PCA
ORE 76799	OR	Linn	44.42, -121.95	A. Roach	sn	Nonstip. E. greenei	PCA
OSC 10974	OR	Lake	42.70, -120.55	J. Elder	sn	Nonstip. E. greenei	PCA
OSC 213401	OR	Jackson	42.08, -122.72	S. Sundberg	2638	Nonstip. E. greenei	PCA
OSC 74849	OR	Klamath	42.95, -122.10	W. Baker	sn	Nonstip. E. greenei	PCA
OSC 168921	OR	Jackson	42.03, -123.83	M. Paetzl	sn	Nonstip. E. greenei	PCA
RENO 52927	NV	Douglas	39.09, -120.04	F. Hillman	sn	E. bloomeri	PCA
RENO 52922	NV	Aspen	39.46, -119.91	N. Peterson	432	E. bloomeri	PCA
RENO 52921	NV	Storey	39.31, -119.67	B. Larson	118	E. bloomeri	PCA

Accession #	State	County	Latitude, Longitude	Collector	Coll. #	Taxon	Included in
RENO 52918	CA	Nevada	39.39, -120.09	P. Pabaubaue	sn	E. bloomeri	PCA
RENO 52903	CA	Nevada	39.17, -120.14	P. A. L.	3078	E. bloomeri	PCA
RENO 52905	CA	Mono	37.73, -118.95	M. Williams	86-80-1	E. bloomeri	PCA
RENO 52904	OR	Klamath	43.495, -121.923	R. Halse	6326	E. bloomeri	PCA
RENO 61937	NV	Douglas	39, -119.9	A. Tiehm	17218	E. bloomeri	PCA
RENO 52910	NV	Humboldt	41.64, -119.26	J. Nachlinger	2153	E. bloomeri	PCA
RENO 52920	CA	Siskiyou	41.58, -121.58	M. Williams	85-69-1	E. bloomeri	PCA
RENO 52931	NV	Washoe	39.61, -119.98	M. Williams	86-74-1	E. bloomeri	PCA
RENO 52924	NV	Douglas	39.09, -120.04	P. Kennedy	sn	E. bloomeri	PCA
RENO 56401	CA	Mono	38.25, -119.09	W. Billings	2189	E. bloomeri	PCA
RENO 52929	NV	Washoe	39.59, -119.93	M. Williams	7180	E. bloomeri	PCA
RENO 52923	NV	Carson City	39.16, -119.89	J. Sulman	sn	E. bloomeri	PCA
RENO 52928	CA	Siskiyou	42.68, -124.44	G. Butler	1823	E. bloomeri	PCA
RENO 52913	NV	Washoe	39.46, -119.91	A. Heller	sn	E. bloomeri	PCA
RENO 52917	NV	Washoe	39.34, -119.92	L. Asche	sn	E. bloomeri	PCA
RENO 52915	NV	Washoe	39.95, -119.80	A. Heller	sn	E. bloomeri	PCA
OSC 10973	CA	Siskiyou	41.32, -122.48	H. Heller	sn	E. greenei	
WTU 364983	WA	Kittitas	47.38, -120.88	D. Knoke	972	Nonstip. E. greenei	
WTU 373866	WA	Kittitas	47.52, -121.03	D. Knoke	1682	Nonstip. E. greenei	
WTU 334369	WA	Kittitas	47.06, -121.04	C. Bjork	2807	Nonstip. E. greenei	
WTU 395933	OR	Harney	42.63, -118.58	J. Smith	6967	Nonstip. E. greenei	
WTU 75200	WA	Okanogan	48.44, -120.47	C. Hitchcock	8096	E. greenei	
WTU 273003	WA	Chelan	47.43, -120.76	A. Kruckeberg	6393	Nonstip. E. greenei	
WTU 6447	WA	Chelan	47.43, -120.76	S. Blake	sn	Nonstip. E. greenei	
WTU 190538	WA	Chelan	48.09, -120.33	G. Ward	37	E. greenei	
WTU 232779	WA	Klickitat	45.97, -122.86	W. Suksdorf	sn	E. bloomeri	
WTU 129467	WA	Yakima	46.23, -120.82	V. Heidenreich	sn	E. bloomeri	
WTU 6728	WA	Yakima	46.2, -121.49	S. Blake	sn	E. bloomeri	
WTU 6485	WA	Chelan	47.83, -120.57	G. Morrill	298	E. bloomeri	
WTU 397473	OR	Harney	43.59, -119.06	N. Otting	3045	E. bloomeri	
WTU 131415	OR	Klamath	42.95, -122.1	W. Baker	6237	Nonstip. E. greenei	
WTU 278580	OR	Baker	44.78, -117.83	B. Bafus	405	Nonstip. E. greenei	
WTU 223789	OR	Jackson	42.04, -122.89	K. Chambers	2307	Nonstip. E. greenei	
WTU 217980	WA	Klickitat	46.2, -121.49	A. Kruckeberg	sn	E. bloomeri	
WTU 7201	WA	Okanogen	48.45, -119.63	C. Fiker	459	E. bloomeri	
WTU 271120	WA	Yakima	46.45, -120.86	E. Hunn	735	E. bloomeri	
WTU 6864	WA	Yakima	46.46, -120.74	J. Thompson	11 130	E. bloomeri	
WTU 417256	WA	Kittitas	43.3007, -120.7612	R. Olmstead	sn	Nonstip. E. greenei	
WillU 21706	OR	Hood River	45.5, -121.6	M. Peck	20129	E. greenei	
WillU 18176A	OR	Wallowa	45.23, -117.27	M. Peck	18516	E. greenei	
WTU V051856	OR	Klamath	42.95, -122.1	J. Thomson	135	E. greenei	
WTU V051855	OR	Klamath	42.95, -122.1	W. Baker	62312	E. greenei	
WTU V051863	WA	Kittitas	47.24, -120.56	J. Thomson	9752	E. greenei	

Results

Of the characters measured, 16 were found to be statistically significant (One Way ANOVA, $P<0.05$) between the groups (Table 2). Of the 16 significant characters, 7 distinguish non-stipitate *Ericameria greenei* from *E. bloomeri*: leaf apical width, leaf basal width, leaf length/apical width ratio, leaf length/basal width ratio, midnerve angle, heads per branch, and inflorescence length. Six characters are significantly different between stipitate *E. greenei* and other non-stipitate forms: involucre length, involucre width, outer phyllary length, phyllary length/basal width ratio, inflorescence length, and heads per branch. Only involucre length differs significantly between stipitate and non-stipitate *E. greenei*. Three characters that distinguish stipitate *E. greenei* from *E. bloomeri* are not

significantly different between *E. bloomeri* and non-stipitate *E. greenei*: involucre length/width ratio, outer/inner phyllary length ratio, and peduncle length (Table 2).

In the PCA, *Ericameria bloomeri* is easy to distinguish from the other groups. Neither stipitate nor non-stipitate forms of *E. greenei* overlap with *E. bloomeri* (Figure 4). This is also observed when PCA Axis 1 is plotted vs. Axis 3 (data not shown). Furthermore, non-stipitate forms of *E. greenei* from the Owyhee Mountains and from other geographic locations have greater overlap with *E. greenei* than with *E. bloomeri*. Though there is overlap between the two groups of non-stipitate *E. greenei*, these groups fall mostly into the ordination space occupied by stipitate *E. greenei* (Figure 4).

In Idaho non-stipitate *E. greenei* is limited to the Owyhee Mountains and is allopatric with stipitate *E. greenei* north of the Snake River Plain. In Washington the stipitate forms are parapatric to non-stipitate forms of *E. greenei* in Chelan and Kittitas Counties. Only stipitate forms of *E. greenei* are evident in the Wallowa Mountains of northeastern Oregon. Throughout the rest of Oregon and northern California, including the type locality on Mt. Eddy of the Scott Mountains, non-stipitate forms predominate, but stipitate forms regularly occur (near Mt. Hood, on Steens Mountain, in Klamath County and in the Scott Mountains). Only non-stipitate forms are evident in the disjunct population from the Charleston Mountains of southern Nevada. (Table 1, Figure 5).

Table 2. Ranges of the characters measured for each group of plants and their significance. All 130 samples examined are included within the ranges given. Of the 24 characters measured 16 were found to be statistically significant (One Way ANOVA, $P < 0.05$). The final column shows which categories, if any, have statistically significant differences in the given character. *E. greenei* refers to stipitate forms of *E. greenei*

Character	*E. bloomeri*	*E. greenei*	Nonstip. *E. greenei*	Significance	Distinguishes
Gland Stipe Length	None	0-18 µm	None	P = <0.001	E. greenei from others
Leaf Apical 1/3 Width	0.5-4 mm	2-8 mm	2-6 mm	P = <0.001	E. bloomeri from others
Leaf Basal 1/3 Width	0.5-3 mm	1-5 mm	1-5 mm	P = <0.001	E. bloomeri from others
Leaf Apical Length/Width Ratio	9-60.	3.3-15	3-14.	P = <0.001	E. bloomeri from others
Leaf Basal Length/Width Ratio	9-60.	5.2-16.7	4-25.	P = <0.001	E. bloomeri from others
Midnerve Angle	10-45˚	20-90˚	14-85˚	P = <0.001	E. bloomeri from others
Involucre Width	3-10 mm	5-20 mm	4-8 mm	P = <0.001	E. greenei from others
Involucre Length/Width Ratio	1-3.8	0.9-2.1	0.75-2.2	P = <0.001	E. bloomeri from E. greenei
Outer Phyllary Length	2-10 mm	2-17 mm	2-11 mm	P = <0.001	E. greenei from others
Phyllary Basal Length/Width Ratio	2-10.	2-17.	1-11.	P = <0.001	E. greenei from others
Average Heads Per Branch	1-7.1	1-4.	1.3-7.5	P = <0.001	Nonstip. From others
Phyllary Apical 1/3 Width	0.5-1.5 mm	0.5-2 mm	0.5-1.5 mm	P = <0.001	E. greenei from others
Outer/Inner Phyllary Length Ratio	0.31-1.3	0.42-1.7	0.3-2	P = 0.003	E. bloomeri from E. greenei
Involucre Length	5-13 mm	7-17 mm	3-11 mm	P = 0.016	E. greenei from Nonstip.
Peduncle Length	0.5-16 mm	1-15 mm	1-11 mm	P = 0.022	E. bloomeri from E. greenei
Inflorescene Length	9-20 mm	12-20 mm	7-19 mm	P = 0.023	Nonstip. From others
Inner Phyllary Length	5-13 mm	4-15 mm	5-11 mm	P = 0.052	N/A
Gland Diameter	0-14 µm	2-92 µm	9-23 µm	P = 0.052	N/A
Phyllary Apical Length/Width Ratio	2-10.	2-11.	3-16.	P = 0.063	N/A
Number of Phyllary Series	2-3.	2-3.	1-3.	P = 0.087	N/A
Leaf Length	19-45 mm	8-40 mm	20-27 mm	P = 0.094	N/A
Glands	Absent or Presen	Absent or Presen	Present	P = 0.156	N/A
Angle of Branches	90-155˚	90-153˚	120-155˚	P = 0.238	N/A
Basal 1/3 Phyllary Width	1-2 mm	0.5-2 mm	1-1.5 mm	P = 0.689	N/A

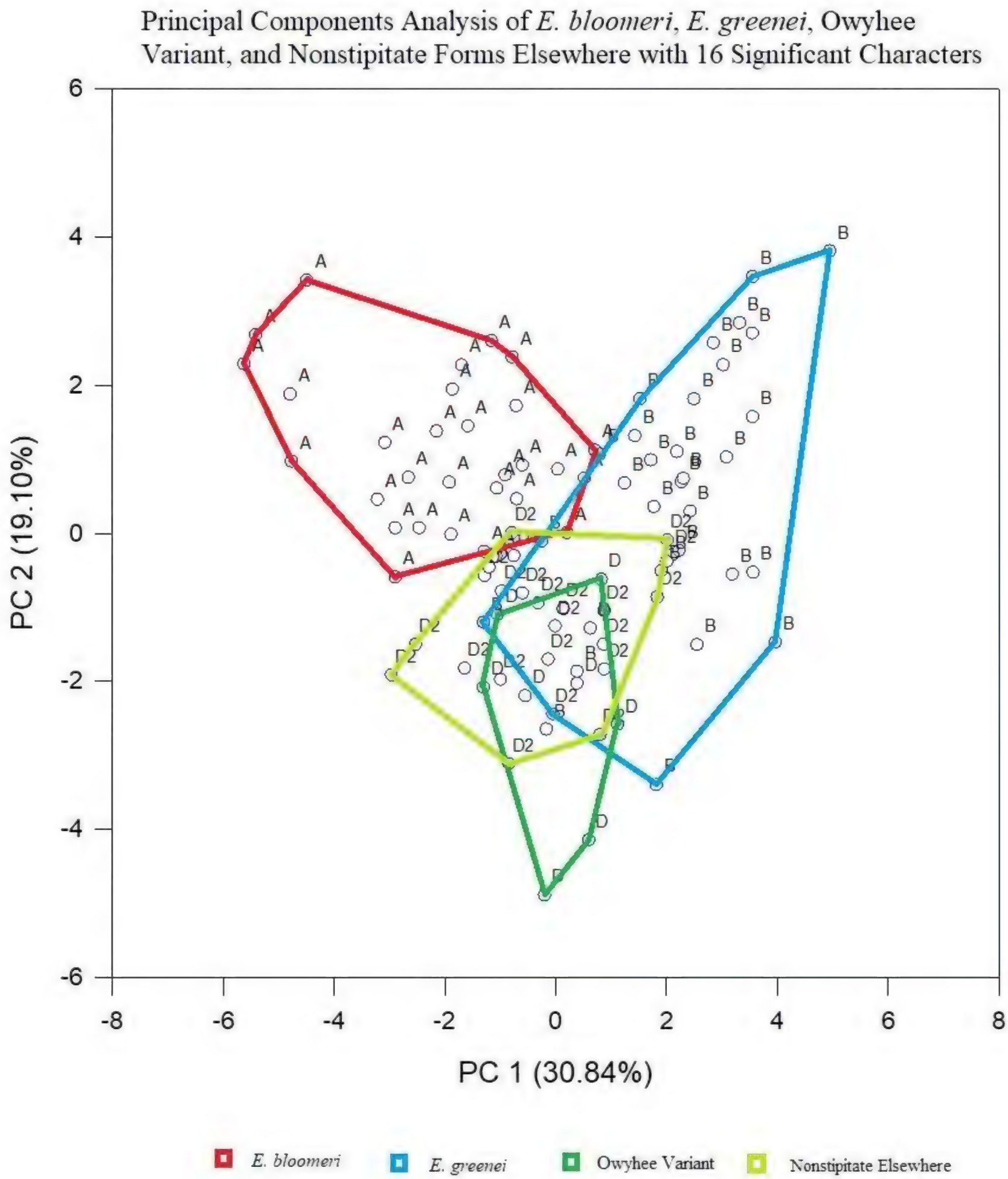

Figure 4. *E. bloomeri* is distinct from the other three population groups. *Ericameria greenei* (stipitate) has considerable overlap with both the Owyhee variant (non-stipitate) and the non-stipitate form found elsewhere. The ordination used the 16 characters shown to be significant (Table 2). The principal components 1 and 2 shown account for 49.94% of variation.

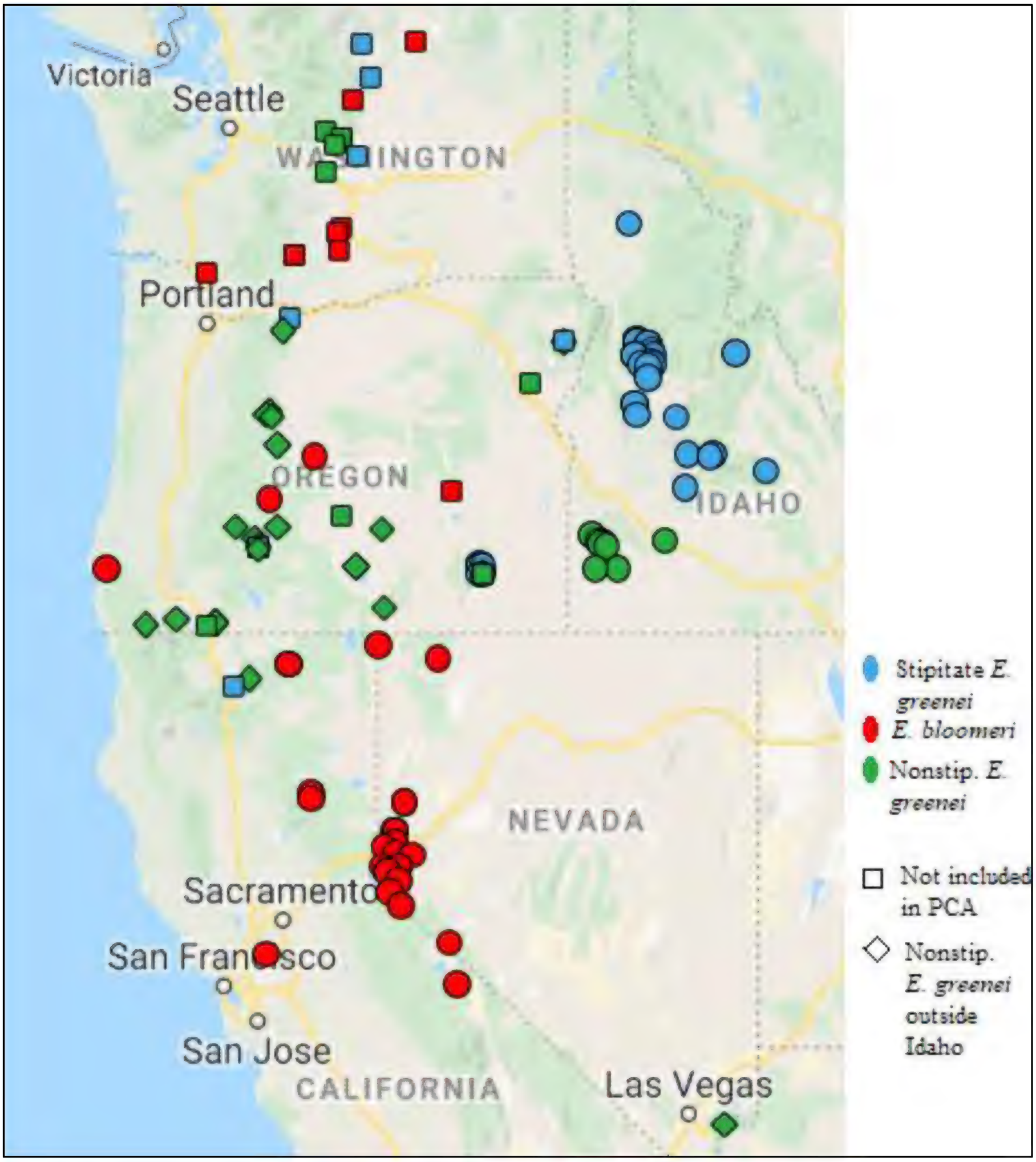

Figure 5. Geographic location of specimens.

Discussion

Ericameria populations from the Owyhee Mountains would be treated in Flora of North America by Urbatsch et al. (2006) as *E. bloomeri*, because they lack stipitate glands (Figures 1 and 3). However, the lectotype of *E greenei* also lacks stipitate glands. Thus, we examined a variety of morphological features to clarify the affinities of stipitate and non-stipitate *E. greenei* throughout the range of *E. bloomeri* and *E. greenei*. Three possible scenarios are evident. First, the Owyhee specimens may represent populations of *E. bloomeri* disjunct from the rest of *E. bloomeri* to the west. Second, the stipitate plants north of the Snake River Plain in Idaho may represent a different variety of *E. greenei*

than the plants from the Owyhee Mountains. Finally, the stipitate and non-stipitate characteristics may be morphological variation insufficient to designate varietal distinction, despite the geographic allopatry of these two forms evident in Idaho.

Owyhee collections appear more like stipitate *Ericameria greenei* than *E. bloomeri,* with wider leaves, and smaller length/width ratios than *E. bloomeri* leaves (Table 2; Legler et al. 2018). The Owyhee variant resembles the non-stipitate form of *E. greenei* found throughout Oregon, Washington and northern California, with disjunct populations in southern Nevada, all, including the type, having leaves with a similar length to width ratio and the same non-stipitate resinous glands (Figure 4). A preliminary One Way ANOVA found only one significant difference among the characters measured between the Owyhee collections and non-stipitate *E. greenei* outside of Idaho, a difference in midnerve angles (data not shown). In the PCA the two groups of non-stipitate *E. greenei* overlap almost completely (Figure 4). This suggests that the Owyhee variant and non-stipitate *E. greenei* collected outside of Idaho represent the same taxonomic entity.

Our research suggests that the non-stipitate Owyhee collections should not be classified as *Ericameria bloomeri* despite having similar non-stipitate resinous glands (Figures 1 and 3). Rather, the non-stipitate *E. greenei* more closely resembles stipitate *E. greenei*, sharing a similar range of the following morphological characters with stipitate *E. greenei*: leaf apical width, leaf basal width, leaf length/apical width ratio, leaf length/basal width ratio, and midnerve angle (Table 2). This is also supported by the PCA of the 16 significant characters (Figure 4) and of all 24 characters (data not shown), in which the non-stipitate form of *E. greenei*, whether from the Owyhee region or elsewhere, overlap considerably with the stipitate form of *E. greenei*, while barely overlapping with *E. bloomeri*. Thus, we conclude that the Owyhee specimens are best classified as *E. greenei* and not as disjunct *E. bloomeri.* Furthermore, use of the "stipitate glands" to distinguish *E. greenei* from *E. bloomeri* (as in Urbatch et al. 2006) is unjustified.

To assess whether varietal distinction between stipitate and non-stipitate forms of *Ericameria greenei* is justifiable we asked first whether other morphological characters shared the same pattern of variation observed with gland form and then whether the forms exhibit consistent geographic variation. Involucre length was the only other character that differed between non-stipitate and stipitate *E. greenei*--the non-stipitate forms having shorter involucres (Table 2). In the PCA while the stipitate and non-stipitate forms of *E. greenei* showed different extremes in the ordination space, a significant degree of overlap was observed suggesting morphological continuity of stipitate and non-stipitate forms, as expected if they represent the same taxonomic entity (Figure 4). Furthermore, distinction between stipitate and non-stipitate samples can also sometimes be unclear in cases where the stipes may be especially small or when there are both stipitate and non-stipitate glands on the leaves of the same plant. WILLU 21706 and WILLU 18176A were scored as stipitate *E. greenei* and labeled in blue in Figure 5, but they produce non-stipitate glands as well as glands with stipes. Thus, stipitate glands may represent mere population variants within otherwise non-stipitate populations.

The two gland forms are clearly allopatric in Idaho with forms lacking stipitate glands occurring only in the Owyhee Mountains southwest of the Snake River Plain and those with stipitate glands north of the Snake River Plain. The stipitate form of *Ericameria greenei* extends through the Wallowa Mountains of northeastern Oregon and into the mountains of northern Washington. Stipitate forms of *E. greenei* also occur sympatrically with non-stipitate forms near Mt. Hood and in Steens Mountain in Oregon and in the Scott Mountains of northern California, where the non-stipitate type of *E. greenei* was collected (Figure 6). Thus, there appears to be allopatric differentiation of these two

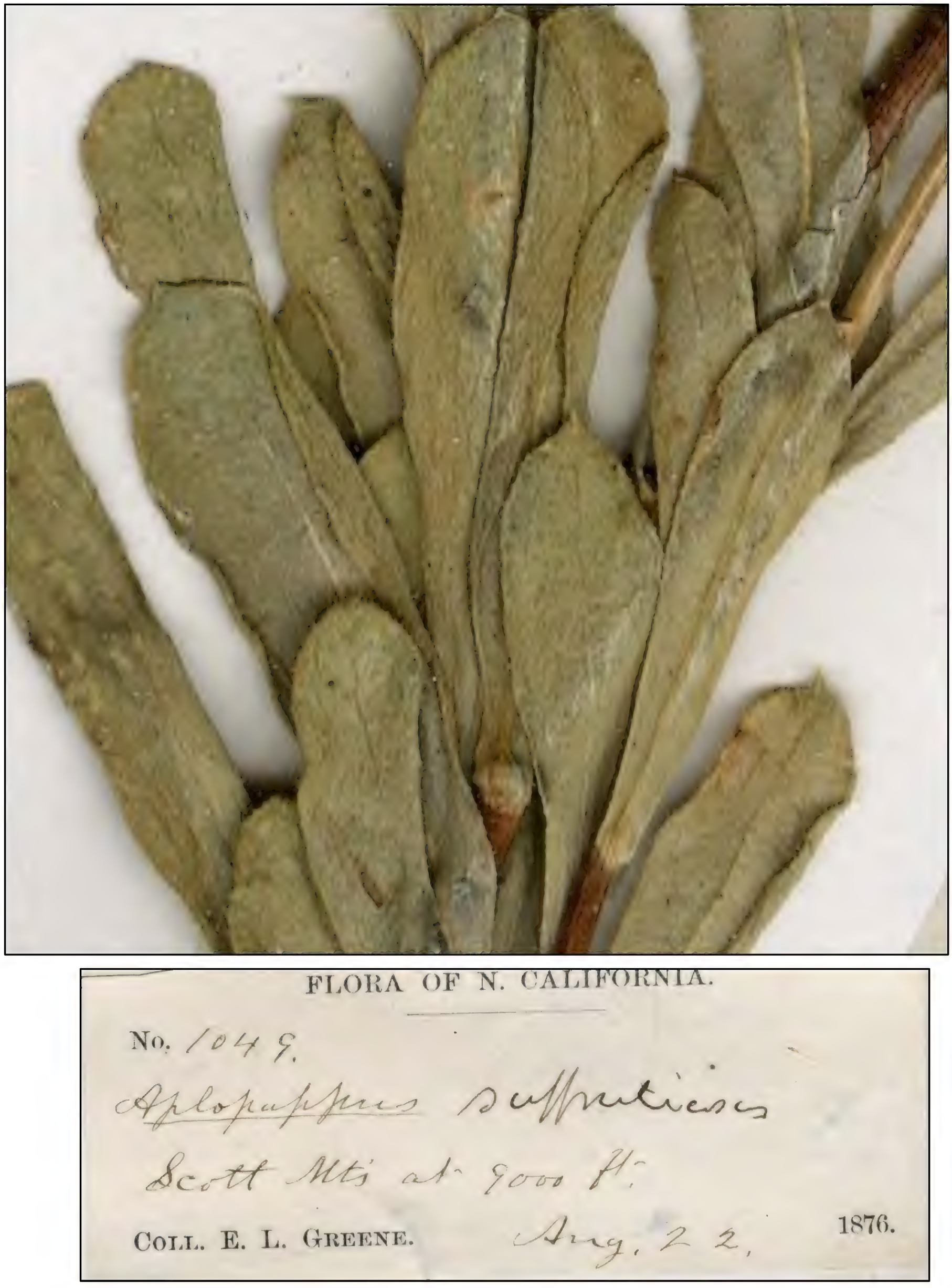

Figure 6. The lectotype collection by E.L. Greene from Mt. Eddy in the Scott Mountains in Siskiyou Co., California with non-stipitate glands.

forms along a border from central Washington to southern Idaho, but presence of both forms throughout much of Oregon and northern California. The Snake River Plain poses a significant barrier to distribution of other plant species (Ertter & Moseley 1992, Holmgren 1972) suggesting that this barrier may have facilitated evolutionary differentiation of varietal forms in *Ericameria* as well.

In his treatment of the Intermountain Flora Cronquist (1994) included *Ericameria greenei* as a variety of *E. bloomeri* under the synonym *Haplopappus bloomeri* var. *greenei* (A. Gray) Cronquist noting that "both varieties embrace glandular and tomentose-puberulent phases that often grow intermingled." Here we have demonstrated that while the glandular forms often "grow intermingled", they also are distinct in their distribution across a border from the Snake River Plain into northcentral Washington appearing as distinct varieties. In our study six of the 121 populations represented in Table 1 clearly exhibited a tomentose phase. Of those all were in stipitate *E. greenei* from northcentral Idaho and eastern Oregon. Hall (1928) recognized tomentose forms in both *E. greenei* and *E. bloomeri*, referring to the "finely tomentose" form of *E. greenei* under the name *Haplopappus mollis* A. Gray) ssp. *mollis* H.M. Hall. Our study sheds no light on whether these forms were "intermingled" with glabrous forms. Though we only observed tomentose forms in stipitate *E. greenei*, it is likely that Hall observed them in non-stipitate *E. greenei*, because he noted the occurrence of stipitate forms as "rare" and gave no indication of co-occurrence of stipitate glands and tomentose forms. These tomentose forms are represented with a variety of synonyms, including *Haplopappus greenei* var. *mollis* (A. Gray) A. Gray, *Hoorebekia greenei* ssp *mollis* (A. Gray) Piper and *Macronema greenei* var. *mollis* (A. Gray) Jeps. In Flora of North America Urbatsch et al. (2006) noted that "a tomentose entity that was recognized as *Haplopappus greenei* subsp. *mollis* differs also in other ways from typical *Ericameria greenei*. It may merit recognition at some level." Our study sheds no light on what those "other ways" might be. Though tomentose forms co-occur with stipitate glands in some instances, we observed many more instances in which stipitate glands occurred in otherwise glabrous plants. We were unable to detect any geographic patterns in tomentose forms, though our sample of tomentose forms was very limited.

We are reluctant to propose varietal rank to the populations of *Ericameria greenei* possessing stipitate glands. Though populations from northern Idaho, northeastern Oregon and northern Washington could easily be assigned to such a novel variety, many populations with stipitate glands throughout Oregon and northern California occurring in sympatry with otherwise non-stipitate forms (e.g. on Steens Mountain or Scott Mountains) would be wrongly assigned based on that single character. Furthermore, the paucity of other morphological distinction between the stipitate and non-stipitate forms (Table 2) argues against assigning varietal rank, as does the PCA (Figure 4), in which both gland forms fall within a single multivariate ordination space. Without a clearer understanding of the genetic basis of stipe formation of glands in *Ericameria* sect. Macronema, or additional morphological characters distinguishing stipitate and non-stipitate *E. greenei* (Figure 4) there remain unclear boundaries within *E. greenei*.

In this study we have rejected the use of stipitate glands as a taxonomic diagnostic for distinguishing *E. greenei* from *E. bloomeri*. The distinctions between *E. greenei* and *E. bloomeri* remain quantitative at best. Our research supports the classification of *Ericameria* specimens from the Owyhee Mountains as *E. greenei* not *E. bloomeri*. We demonstrate allopatric differentiation between stipitate and non-stipitate forms of *E. greenei*, but we hesitate to propose varietal status for the stipitate forms without further evidence. Thus, based on current records, *E. bloomeri* is absent from Idaho.

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ERYTHRANTHE SERPENTINICOLA (PHRYMACEAE), A NEW SERPENTINE-ENDEMIC SPECIES FROM SAN LUIS OBISPO COUNTY, CALIFORNIA

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ABSTRACT

Erythranthe serpentinicola D.J. Keil, **sp. nov.** (Phrymaceae), is described from areas of serpentine soil in west-central San Luis Obispo Co., California. It is a member of *Erythranthe* sect. *Simiolus* and is disjunct from *E. pardalis,* a species of the Sierra Nevada foothills, to which it is most similar and perhaps most closely related. Both *E. serpentinicola* and *E. pardalis* are slender annuals with relatively small flowers. Calyces of both species are often dotted with dark red spots, and both are puberulent with delicate gland-tipped trichomes. Both occur primarily on serpentine soils. *Erythranthe serpentinicola* differs from *E. pardalis* in having usually sessile distal cauline leaves, a dense puberulence of fine, spreading glandless trichomes in addition to the gland-tipped trichomes, generally shorter fruiting pedicels, puberulent rather than glabrous styles that are longer exserted than those of *E. pardalis*, and longer corollas that are exserted to a greater extent beyond the calyx.

In the spring of 1979, I collected a yellow-flowered monkeyflower from a serpentine area in the Irish Hills above San Luis Obispo (*Keil 13058*). The Irish Hills are the western half of the San Luis Range, a ridge of the South Coast Range separated from the Santa Lucia Range by the Los Osos and San Luis Valleys. My attempt to identify the plant led me to the polymorphic *Mimulus guttatus* DC. complex, where with some doubt I determined the plant to be *M. nasutus* Greene. Some years later (date not recorded) Dr. David Thompson pencil-annotated a sheet of this collection (OBI138330) as *M. guttatus*.

Based on morphology and molecular phylogenetic data Barker et al. (2012) revised the generic circumscription of *Mimulus*, resurrecting the formerly monospecific genus *Erythranthe* Spach and greatly expanding it to encompass numerous species previously classified in *Mimulus*, including the members of the *M. guttatus* complex. In an accompanying paper Nesom (2012) critically examined *Erythranthe* sect. *Simiolus* (Greene) Nesom, including the *M. guttatus* complex. Nesom restricted the application of the name *Erythranthe guttata* (DC.) Nesom [=*Mimulus guttatus*] to a more homogeneous set of plants and recognized numerous entities that had formerly been treated as races or forms of *M. guttatus* as distinct species of *Erythranthe*. As I examined and sought to understand Nesom's revised monkeyflower taxonomy, I noted that he had cited a duplicate of *Keil 13058* (TEX) as *Erythranthe arenicola* (Pennell) Nesom, one of the segregate species.

In preparation of the manuscript for the second edition of the Vascular Plants of San Luis Obispo County, California (Keil and Hoover in prep.), I attempted to test Nesom's revised taxonomy of this complex with monkeyflowers that I encountered in my field work. I quickly realized that *Mimulus guttatus*, as I had been applying it, encompassed several readily distinguishable entities. I struggled, however, with the concept of *Erythranthe arenicola*, which seemed to encompass disparate elements. During my field work I encountered two additional populations similar to the one represented by *Keil 13058.* Both were also found on soils derived from serpentine substrates in the vicinity of San Luis Obispo. Despite my misgivings I tentatively determined them to be *E. arenicola*.

After examining additional material, Nesom (2019) reevaluated *E. arenicola* and determined that it is actually a depauperate form of a more widespread species, *E. grandis* (Greene) Nesom, that is restricted to sandy, coastal sites in Monterey Co., California. He made no mention of the plant I had collected from an upland serpentine habitat in San Luis Obispo Co. In subsequent correspondence Dr. Nesom acknowledged that he had been mistaken and that the San Luis Obispo Co. plants are not at all the same as those from Monterey Co. He instead noted that they are similar to but not the same as *E. pardalis* (Pennell) Nesom of the Sierra Nevada foothills. Both the San Luis Obispo plants and *E. pardalis* are apparently restricted to serpentine substrates. Further investigation of photos and herbarium material revealed several features by which these plants differ. I therefore am recognizing the San Luis Obispo County plants as a new, serpentine-endemic species.

ERYTHRANTHE SERPENTINICOLA D.J. Keil, **sp. nov. TYPE: USA. California.** San Luis Obispo Co.: Irish Hills Natural Reserve, serpentine springs area on slope above Froom Creek Trail, a short distance E of junction with Poppy Trail, locally common on moist soil with *Chorizanthe breweri* and *Cirsium fontinale* var. *obispoense* on exposed sites around spring, also observed nearby on lower Poppy Trail in moist trail margins, corolla golden yellow, lower lip with red spots, 35.25259°, -120.71381°, 205 m, 22 Apr 2019, *D.J. Keil 35581* (holotype: OBI147660 [Fig. 1]; 4 isotypes to be distributed).

Similar to *Erythranthe pardalis* in its serpentine habitat, annual duration, small flowers, spotted calyces, and vestiture of delicate, gland-tipped trichomes but different in its sessile distal cauline leaves, a dense puberulence of glandless trichomes in addition to the gland-tipped ones, shorter fruiting pedicels, puberulent rather than glabrous, longer-exserted styles, and longer, longer-exserted corollas.

Additional specimens examined. California. San Luis Obispo Co.: Upper Prefumo Canyon Road, grassy area with scattered patches of chaparral, locally abundant on rock outcrop, flowers yellow with red dots, [35.255251°, -120.760226°], [360 m], 29 Apr 1979, *Keil 13058* (OBI [Fig. 2], SBBG, TEX); Laguna Lake Park, San Luis Obispo, serpentine hillside near bog thistle exclosure, local in moist soil, scattered elsewhere, *Erythranthe microphylla* growing nearby, corolla yellow, lower lip with red spots, 35.267147°, -120.683066°, 60 m, 5 May 2017, *Keil 34609* (OBI [Fig. 3], +2 duplicates to be distributed); Irish Hills Natural Reserve, serpentine springs area on slope above Froom Creek Trail, a short distance E of jct with Poppy Trail, locally common on moist soil with *Chorizanthe breweri*, also observed nearby on lower Poppy Trail in moist trail margins, 35.25259°, -120.71381°, 205 m, 17 March 2019, *Keil 35496* (OBI [Fig. 4]).

Annual, 7–40 cm, slender; herbage sparsely to densely puberulent, at least distally, with variable mixture of short, fine, spreading, glandless hairs and delicate gland-tipped hairs, proximally ± glabrous. Stems cylindric, erect or with decumbent bases, simple or branched from proximal to medial nodes. Leaves mostly cauline, basal usually absent at flowering, cauline short-petioled or distal sessile, distalmost sometimes ± connate, blades broadly ovate to ± circular, palmately 3–5-veined, margin entire or shallowly dentate-serrate. Flowers ± evenly distributed from proximal to distal nodes. Fruiting pedicels 10–25 mm. Calyx in flower 5–11 mm, cylindric-campanulate, usually reddened, often with dark-purple spots, in fruit 9–14 mm, ellipsoid to ovoid with throat closed, distal lobe prolonged, straight or moderately downcurved. Corolla 12–20 mm, yellow, throat and lower lip red-dotted, lower lip villous medially, tube-throat funnelform, 7–10(–15) mm, exserted 1–4 mm beyond calyx rim, limb expanded 8–12 mm (when pressed). Anther pairs at slightly different levels; style minutely puberulent, stigma positioned slightly beyond distal anther pair. Capsule ± 5–8 mm, borne on a short gynophore, included within calyx (Figs. 3–6).

Etymology. The epithet serpentinicola is derived from the Latin serpentinus (serpentine rock) and -cola (inhabitant), referring to plants inhabiting soils derived from serpentine rock (Stearn 1966).

Suggested common name. Irish Hills monkeyflower.

Distribution, habitat, and abundance. *Erythranthe serpentinicola* is documented only from three sites in the western South Coast Range in west-central San Luis Obispo Co., California. Two

populations (separated by 2.6 miles (4.2 km)) are documented from the northeastern portion of the Irish Hills. The type locality is located in the immediate vicinity of a serpentine spring in Froom Creek Canyon in San Luis Obispo's Irish Hills Natural Area. The site is surrounded by dense chaparral dominated by *Adenostoma fasciculatum*, *Arctostaphylos obispoensis, Ceanothus cuneatus* var. *ramulosus*, *Pickeringia montana* var. *montana*, *Quercus durata* var. *durata*, and *Salvia mellifera*. Moist soil around the spring was occupied by *Castilleja minor* var. *spiralis, Cirsium fontinale* var. *obispoensis*, and *Salix breweri*. Immediate associates of *E. serpentinicola* included *Allium lacunosum* var. *lacunosum, Chorizanthe breweri*, seedlings of the *Cirsium, Cryptantha clevelandii, Epilobium minutum*, and *Eschscholzia californica.* The second Irish Hills population occupies an upland site located on private land bordering upper Prefumo Canyon Road. The habitat is an open, grassy slope with patches of chaparral. *Erythranthe serpentinicola* was locally abundant around and on serpentine outcrops. The third population occurs about two miles (3.2 km) northeast of the type locality in San Luis Obispo's Laguna Lake Park and Open Space. It is situated on the lower southeastern flank of Cerro San Luis Obispo, which is one of the Morros, a chain of nine volcanic hills and mountains in western San Luis Obispo County. The site is a southwest-facing serpentine grassland with springs featuring *Cirsium fontinale* var. *obispoensis*. *Erythranthe microphylla* (Benth.) Nesom grows in moist soil with the thistles. *Erythranthe serpentinicola* was scattered in shallow soil on the grassy slope.

Soils derived from serpentine parent material are island-like in their occurrence in San Luis Obispo County. Because of their unusual chemistry—high Mg^{++}, low CA^{++} and the presence of toxic metals (e.g., Cr, Hg)—these soils are challenging substrates for plant growth. Various species have evolved features that enable them to grow on serpentine-derived soils. Plants wholly or largely endemic to serpentine soils occur in various combinations on the patches of serpentine in the San Luis Obispo area. Fifteen of these (starred) occur near populations of *Erythranthe serpentinicola*: **Allium lacunosum* var. *lacunosum*, *Aquilegia eximia*, **Arctostaphylos obispoensis*, **Astragalus curtipes*, **Calochortus obispoensis*, **Carex obispoensis*, **Chorizanthe aphanantha*, **C. breweri, *C. palmeri*, **Cirsium fontinale* var. *obispoense*, *Dudleya abramsii* subsp. *bettinae*, **D. abramsii* subsp. *murina*, *Hesperocyparis sargentii*, **Layia jonesii*, **Lomatium parvifolium*, **Monardella palmeri, *Quercus durata* var. *durata*, **Salix breweri*, *Sidalcea hickmanii* subsp. *anomala*, and *Zeltnera muehlenbergii*. The type locality of *E. serpentinicola* is close to that of the recently described *Chorizanthe aphanantha* (Nelson et al. 2019). Indeed *C. aphanantha* was found growing on trail margins within a few meters of *E. serpentinicola*.

Phenology. *Erythranthe serpentinicola* is a spring-flowering annual, and germination is dependent on adequate winter precipitation. Flowering specimens have been collected from 17 March to 9 May. Flowering is expected to extend from about the beginning of March until late May depending on seasonal precipitation patterns.

Conservation assessment. *Erythranthe serpentinicola* is documented at present from just the three populations represented by the specimens cited above. Kristen Nelson (pers. comm.) has observed a fourth population near an abandoned chromite mine in the Irish Hills Natural Reserve, but no specimens currently document this occurrence. It is likely that additional populations occur in serpentine soils in the San Luis Obispo area. The two most widely separated documented populations are about 4.4 miles (7.1 km) apart. Two of the known populations occur in open space areas owned and managed by the City of San Luis Obispo. The third is on private ranch land. The total areal extent of the populations is unknown but is unlikely to exceed a few acres. Potential threats include foot traffic, grazing, fire, and (for the site on private land) changes in land usage. Recognition of *E. serpentinicola* as a rare and potentially endangered species seems warranted; I recommend it be considered by the California Native Plant Society for California Rare Plant Rank 1B.1. When evaluated using IUCN (2000) Red List criteria, *E. serpentinicola* qualifies as Endangered (EN) – High risk of extinction in the wild, based on extent of occurrence estimated to be less than ~100 km^2.

Figure 1. Holotype of *Erythranthe serpentinicola*, *Keil 35581* (OBI147660).

Figure 2. Paratype of *Erythranthe serpentinicola*, *Keil 13058* (OBI138330).

Figure 3. Paratype of *Erythranthe serpentinicola*, *Keil 34609* (OBI147662).

Figure 4. Paratype of *Erythranthe serpentinicola*, *Keil 35496* (OBI147661).

Figure 5. Habit and serpentine gravel habitat of *Erythranthe serpentinicola*, from type locality.

Figure 6. Flowers and distal bracts of *Erythranthe serpentinicola*, from type locality.

Figure 7. Flowers and distal bracts of *Erythranthe serpentinicola*, from type locality.

Relationships. *Erythranthe serpentinicola* is a member of *Erythranthe* sect. *Simiolus* and is similar to *E. pardalis* (Pennell) Nesom, a species largely restricted to serpentine soils of the Sierra Nevada foothills. *Mimulus pardalis* Pennell was recognized as a distinct species by Pennell (1951) but was subsumed within *M. guttatus* sensu lato or not mentioned at all in subsequent floras (Munz & Keck 1959; Thompson 1993, 2012). Nesom (2012) resurrected this species as *Erythranthe pardalis* and synonymized *M. cupriphilus* Macnair with it. Fraga (2018), Rabeler et al. (2019), and Nesom and Fraga (2019) accepted *Erythranthe* as a genus distinct from *Mimulus* and recognized *E. pardalis* as a distinct species.

Both *Erythranthe serpentinicola* and *E. pardalis* are slender annuals with relatively small flowers. Calyces of both species are often dotted with dark red spots, and both have an indument of delicate gland-tipped trichomes. Both occur primarily on serpentine soils, though *E. pardalis* is also known from copper mine tailings, and one population in Tehama County was collected from a basaltic substrate. Leaves of *E. pardalis* are usually short-petioled more or less throughout, whereas distal leaves of *E. serpentinicola* are usually sessile, and the bract-like distalmost leaves may be connate. Herbage of *E. serpentinicola* is at least distally densely puberulent with fine, spreading glandless trichomes in addition to the gland-tipped trichomes. Pedicels of *E. pardalis* may elongate to as much as 60 mm in fruit whereas those of *E. serpentinicola* reach a maximum of 25 mm and often are shorter. Styles of *E. serpentinicola* are sparsely puberulent and are longer exserted than those of *E. pardalis*, and their corollas are longer, and further exserted beyond the calyx. The two species are strongly disjunct, with *E. pardalis* occurring in the Sierra Nevada foothills from Tehama Co. to Tuolumne Co. whereas *E. serpentinicola* is restricted to a small area of the southern South Coast Range in San Luis Obispo Co. Whether the similarities of *E. serpentinicola* and *E. pardalis* are a result of common ancestry or are independently derived has not been determined.

Several other species of *Erythranthe* occur on soils derived from serpentine parent materials. I have collected annual *E. microphylla* and perennials *E. grandis* and *E. guttata* from serpentine soils in the vicinity where *E. serpentinicola* occurs, but none of these is restricted to these soils. In addition to *E. pardalis* and *E. serpentinicola*, species of *Erythranthe* wholly or in part restricted to serpentine include annuals *E. glaucescens* (Greene) Nesom, *E. percaulis* Nesom, *E. trinitiensis* Nesom, and *E. nudata* (Curran ex Greene) Nesom, and perennials *E. linearifolia* (A.L. Grant) Nesom & Fraga, and *E. willisii* Nesom. At least some of these species have independently adapted to serpentine substrates, but perhaps some share a common adaptive history.

The partitioning of Phrymaceae that resulted in the segregation of *Erythranthe* as a genus separate from *Mimulus* remains controversial (Lowry et al. 2019; Nesom et al. 2019). Numerous biosystematic studies have been published for taxa treated as the *Mimulus guttatus* complex, and some authors continue to use the name *M. guttatus* with a traditional broad species concept (e.g., Popovic & Lowry 2020). On the other hand editors and authors of various floras have adopted the revised generic concepts for Phrymaceae (e.g., Fraga 2018; Rabeler et al. 2019; Nesom & Fraga 2019). Unfortunately epithets published in one genus (e.g., *Erythranthe*) do not automatically transfer to the other (*Mimulus*). This issue with the competing generic and species concepts sometimes deprives users of monkeyflower taxonomy the flexibility to adopt taxonomic circumscriptions without having to formally propose new combinations (e.g., Keil 2019). So in proposing *Erythranthe serpentinicola* as a species new to science I recognize that it may be overlooked or disregarded by those whose favored genus is *Mimulus* and whose concept of *Mimulus guttatus* is broad and inclusive.

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MENTZELIA PECTINATA VAR. *CHRYSOPETALA* (LOASACEAE), A YELLOW-PETALED RACE FROM WEST-CENTRAL CALIFORNIA

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ABSTRACT

Mentzelia pectinata Kellogg var. ***chrysopetala*** Keil & Brokaw, **var. nov.**, is a yellow-petaled race of the otherwise orange-petaled *M. pectinata*, a species endemic to central California. The yellow- and orange-petaled varieties are largely allopatric, with var. *chrysopetala* nearly restricted to San Luis Obispo County, whereas var. *pectinata* extends eastward into the dry hills and mountains around the southern end of the San Joaquin Valley, including eastern portions of San Luis Obispo County. Petals of var. *chrysopetala* are golden yellow, usually with orange bases, unlike the petals of var. *pectinata*, which are coppery orange with red-orange bases. We designate a neotype for *M. pectinata* because original material, which presumably was in CAS, apparently is no longer extant; the holotype was probably destroyed in the 1906 San Francisco earthquake and fire.

Mentzelia pectinata Kellogg is an annual species endemic to the southern part of California's San Joaquin Valley and the surrounding hills and mountains of the South Coast Range, Transverse Range, and foothills of the southern Sierra Nevada. In spring growing seasons with abundant rainfall, these plants often form large populations, and the mass displays of their flowers form conspicuous splashes of color across the landscape. The species exhibits two strikingly different flower color forms. Plants from a large part of its range have coppery-orange petals with red-orange bases. Plants from the southern Diablo Range through central San Luis Obispo County and south-central Monterey County have golden yellow petals, usually with orange bases.

Taxonomic treatments of these plants have varied. Kellogg (1863) originally described *Mentzelia pectinata* with "flowers of a shining golden color, with a lustrous metallic hue. shading from a deep, vivid orange to a burnt carmine center." Jepson (1925, 1936) treated *M. pectinata* as part of a broadly defined *M. gracilenta* Torr. & A.Gray, describing the petals of the species as "yellow with orange base." Munz (1959) recognized *M. pectinata* and described the petals as "orange above, coppery-red toward base." Hoover (1970) treated the orange-flowered plants as *M. pectinata* and the yellow-flowered plants as *M. gracilenta*. He noted that that flower color appears to be the only reliable differentiation between the two kinds of plants, but that they are distinct ecologically, geographically, and apparently genetically. Brokaw (2016) distinguished diploid *M. pectinata* from tetraploid *M. gracilenta* using several characters, including (1) orange petals (in most collections of *M. pectinata*, absent in *M. gracilenta*), (2) bracts with white bases (in most collections of *M. gracilenta*, absent in *M. pectinata*), and (3) elevation/habitat (*M. pectinata* occurs at lower elevations than *M. gracilenta* where the ranges overlap in San Luis Obispo County).

Zavortink (1966), in an unpublished dissertation, provided evidence from a biosystematic investigation that the yellow-flowered and orange-flowered plants are two races of a single diploid species: "Hybrids between the two morphological races of *Mentzelia pectinata* showed some slight pairing irregularity in a few instances, but little or no reduction in fertility as indicated by pollen analyses and seed set." This contrasted with the results of her controlled crossing experiments that showed that interspecific crosses between *M. pectinata* and the tetraploid *M. gracilenta* were unsuccessful or that interspecific triploid hybrids had much reduced fertility. But she made no mention of heritability of flower color. She also found that populations of the yellow-flowered race often included a small proportion of orange-flowered individuals that varied from 30:1 yellow- to orange-flowered individuals in years with ample precipitation to fewer than 100:1 in drier years. Zavortink also commented that "variation within *Mentzelia pectinata* is clinal. In the northwest portion of the range the individuals have small yellow flowers (petals 8–14 mm long) with retuse petal tips and large seeds (1.4 mm long and 1.2 mm wide), 20–25 seeds per capsule. In the southwest section of the range the other extreme of the cline has larger flowers with deep orange petals (12–20 mm long) with mucronate tips and small seeds (1.2 mm long and 1.0 mm wide), 30–38 seeds per capsule." However, Zavortink presented no data that demonstrated this to be clinal variation. In her study she did not recognize any infraspecific taxa.

Brokaw (2009) and Brokaw and Hufford (2010a, 2010b) investigated phylogenetic relationships within *Mentzelia* sect. *Trachyphytum*. Yellow-flowered and orange-flowered populations of *M. pectinata* were recovered as a monophyletic lineage closely allied to *M. congesta* Torr. & A.Gray (Brokaw & Hufford 2010a), whereas *M. gracilenta* was hypothesized to be an allopolyploid hybrid of *M. pectinata* and *M. congesta* (Brokaw & Hufford 2010b). A yellow-flowered population of *M. pectinata* evidenced past nuclear introgression with *M. congesta* (Brokaw & Hufford 2010a), and all sampled populations of *M. gracilenta* possessed nuclear DNA from *M. congesta*, suggesting that the yellow phenotype could be promoted by genetic contributions from *M. congesta*.

In both editions of *The Jepson Manual* (Prigge 1993; Brokaw, Schenk, & Prigge 2012), *Mentzelia pectinata* was treated as a species with orange to yellow petals with red to orange bases, but the geographic pattern to this variation was not discussed. We think it is important to address this issue before publication of the second edition of the *Vascular Plants of San Luis Obispo County, California* (Keil & Hoover in prep.). We believe that the yellow-flowered and orange-flowered races of *M. pectinata* are worthy of formal taxonomic recognition. In so doing, we acknowledge their close relationship as evidenced by their interfertility and close phylogenetic relationship. They are readily distinguishable and have allopatric distributions. We have chosen to recognize them as varieties rather than subspecies because the rank of variety has been more frequently used in *Mentzelia* than has subspecies. We consider the use of variety and subspecies to be equivalent in practice, though we recognize their nomenclatural independence and hierarchical relationship (Turland et al. 2018).

MENTZELIA PECTINATA Kellogg var. **CHRYSOPETALA** D.J. Keil & Brokaw, **var. nov.** (Figs. 1, 2).
TYPE: **California**. San Luis Obispo Co: Shell Creek Road, 1.5 mi N of Highway 58, 35.478693°, -120.329352° (WGS84), 410 m, steep roadcut next to road, above valley of Shell Creek, foothill woodland, 4 Apr 2016, *D.J. Keil 33903* with Kathleen Keil (holotype: OBI; isotypes to be distributed).

Flowers of *Mentzelia pectinata* var. *chrysopetala* are readily recognizable in having golden-yellow petals, usually with orange bases (Fig. 2), in contrast to those of var. *pectinata*, which have coppery-orange petals with red-orange bases (Fig. 3).

Annual, 6–60 cm tall. Stems erect or ascending, simple proximal to inflorescence or branched from proximal and/or distal nodes, puberulent with fine, spreading, minutely glochidiate trichomes, epidermis pale, sometimes exfoliating in age. Leaves basal and cauline, basal sometimes absent at flowering; proximal leaves petioled, distal sessile, blades 1–10 cm long, 1–35 mm wide, linear to

oblong-lanceolate to lanceolate in outline or distal sometimes ovate, margins shallowly to deeply pinnately lobed, often to near narrow rachis, with numerous triangular to linear-oblong lobes or sometimes coarsely and shallowly few-lobed or -toothed with wide rachis and proximally widened teeth or lobes, rarely distal entire; abaxial face finely puberulent to pilose with slender, erect, glochidiate trichomes, midrib and sometimes surface hispid to hirsute with scattered, coarse, pustulate-based, glochidiate trichomes; adaxial face and margins hispid-hirsute with pustulate-based, glochidiate trichomes and sometimes puberulent with more slender trichomes as well. Flowers in cymose clusters (solitary) at tips of main stem and branches; bracts leaf-like, green throughout, pinnately or sub-palmately lobed or toothed (entire), terminal lobe or tooth prolonged. Ovary 5–10 mm in flower, narrowly cylindric or slightly expanded distally, finely pilose and densely puberulent with spreading glochidiate trichomes; sepals 6–10 mm long, narrowly to broadly lanceolate, acuminate, abaxially hispid-hirsute and finely puberulent; petals 8–18 mm long, obovate, emarginate to rounded or mucronate, golden yellow (rarely coppery orange), usually proximally orange, occasionally unmarked at base, on dry specimens fading to dull tan with darker veins; anthers and filaments pale yellow; styles and stigmas pale yellow.

Paratypes. California. Monterey Co.: hills, western edge of Hames Valley, [35.891998°, -120.933236°], 11 Apr 1958, *Hardham 3016* (SBBG); hills, western edge of Hames Valley, Bradley-Jolon Rd., [35.891998°, -120.933236°], flowers yellow with red at base of petals, 7 Apr 1959, *Hardham 4201* (CAS, JEPS, RSA, SBBG). San Luis Obispo Co.: Upper reaches of Commatti Cyn, 1.6 mi N of direct road from La Panza to Creston, 16 May 1955, *Bacigalupi 5139* with Robbins and Harrison (CAS, OBI, UC); Shell Creek Road near Hwy 58, 35.478599°, 120.329302°, 9 May 2006, *Brokaw 212* (ACU, WS); Paso Robles River Road along Salinas River S of Creston Road, 35.624285°, 120.680431°, 9 May 2006, *Brokaw 213* (ACU, WS); Fernandez Creek on La Panza-Shandon Road, [35.458034°, -120.333600°], 30 Mar 1947, *Hoover 6834* (CAS, OBI); Cottonwood Pass, near summit, [35.780242° -120.207089°], 2 Apr 1949, *Hoover 7577* (CAS, OBI); between San Juan River and Carrizo Plain, 11 Apr 1949, *Hoover 7586* (CAS, OBI); just E of San Juan River on road from La Panza to Simmler, 21 Apr 1949, *Hoover 7608* (CAS, OBI); between San Juan River and Carrizo Plain, [35.359°, -120.0711°], 20 Apr 1952, *Hoover 8149* (CAS, OBI, UC); between San Juan River and Carrizo Plain on Hwy 58, [35.382262°, -120.121242°], 5 Apr 1967, *Hoover 10358* (CAS, OBI); Shell Creek Road, ca 1/2 mi N of jct with California Rte 58, 9 Apr 1995, *Keil 24782* with K. Keil (OBI); Shell Creek Road, ca 1/2 mi N of jct with California Rte 58, 35.46411°, -120.33005°, 15 Apr 1995, *Keil 24900* with K. Keil (OBI); Shell Creek Road N of Hwy 58 where road cuts against base of hill, vicinity of 35.4790°, -120.3282°, 20 Apr 2001, *Keil 29339* with K. Keil (OBI); between San Juan River and Carrizo Plain, Hwy 58, just E to ca. 0.25 miles E of San Juan Creek bridge, S side of highway, 35.386951°, -120.146136°, 11/12 Apr 2008, *Keil 30499* with Andreano, Walgren, and Sims (OBI, UC); Shell Creek Road N of Hwy 58, 35.47895°, -120.329285°, 7 Apr 2012, *Keil 31246* (OBI, SD); Shell Creek Road, 2 mi from jct with Hwy 58, 18 Apr 1981, *Luckow 665* (OBI); Red Eagle Mine, 1 mi E, 12 mi S of Shandon [35.472564°, -120.378998°], 5 May 1952, *McMillan 103* (CAS, OBI[2]). Coordinates in brackets were estimated from label data.

Etymology. The specific epithet is a compound derived from Greek roots: *chrysos* - gold + *petalon* - petal, describing the golden-yellow petals (Fig. 1) that distinguish the newly-described variety.

Common names. We recommend Obispo Blazing Star as the common name for *Mentzelia pectinata* var. *chrysopetala*. The common name San Joaquin Blazing Star is already in use for *Mentzelia pectinata* (e.g., Calflora 2020) and we recommend that it be restricted to var. *pectinata*.

Figure 1. Holotype of *Mentzelia pectinata* var. *chrysopetala*.

Figure 2. *Mentzelia pectinata* var. *chrysopetala*. A. Close-up of flowers showing adaxial faces of petals. B. Close-up of inflorescence showing bracts and abaxial faces of sepals and petals.

Figure 3. *Mentzelia pectinata* var. *pectinata*. A. Close-up of flowers. B. Close-up of inflorescence showing bracts and abaxial faces of sepals and petals.

Figure 4. Neotype of *Mentzelia pectinata* Kellogg.

Morphology, ecology, and geography. The ranges of var. *chrysopetala* and var. *pectinata* are essentially allopatric. Hoover (1970) described the range of and flower color of var. *chrysopetala* [as *M. gracilenta*]: "In crumbling shale gravel, calcareous clays, or calcareous sandy loams, usually on steep slopes, frequent from Cottonwood Pass to near Creston and Caliente Mt., but absent from Temblor Range. The yellow petals often, but not always, have an orange base." These populations occur largely in the drier portions of the foothill woodland-chaparral zones of the southern South Coast Range.

This contrasts with Hoover's description of the range [in San Luis Obispo County] and flower color of *Mentzelia pectinata* [here treated as *M. pectinata* var. *pectinata*]: "Gypseous clay soils, Temblor Range, Caliente Range, and hills bordering Cuyama Valley. The plants usually grow on slopes which are otherwise nearly barren, and in a year of good rainfall are abundant and showy. The petals are vivid orange, always with a copper red base. The nature of the relationship between this species and *M. gracilenta* is an unsolved enigma. Flower color seems to be the only difference which is completely reliable; yet the two kinds of plants are completely distinct ecologically, geographically, and apparently genetically. Even in the Caliente Range, which is the only known area where they occur relatively near each other, there are no mixed colonies, intergrades as to flower color, evident hybrids, or any sort of evidence of interfertility. Unfortunately, it is usually impossible to determine the flower color from herbarium specimens."

Hoover's last observation is indeed a problem for dealing with specimens lacking flower color data on the labels. Because determining the identity of historic populations that lack flower color data is not possible, the varietal identity of some outlying populations is uncertain. *Mentzelia pectinata* var. *chrysopetala* is nearly endemic to San Luis Obispo County. Two collections document its occurrence in the hills bordering the western edge of the Hames Valley in southern Monterey County. Hoover documented it from the Cottonwood Pass area in the northeastern corner of San Luis Obispo County, and it likely occurs in nearby areas of Kern, Kings, and Monterey counties. A collection from the hills southwest of Kettleman City in Kings County (*Reveal 4380*, CAS, RSA) lacks flower color data and cannot be determined to variety. Specimens from the Annette-Choice Valley area along the San Luis Obispo-Kern Co. line to Cholame similarly lack flower color data.

Hoover did not cite any specimens of *Mentzelia gracilenta* [*M. pectinata* var. *chrysopetala*] from the Caliente Range, and none of his collections from the Caliente Range bear the name *M. gracilenta*. We have not observed any populations or located any specimens of var. *chrysopetala* that would verify its presence in that range.

Zavortink (1966) commented in some detail on geographical and seasonal patterns of variation in *Mentzelia pectinata*:

> Variation within *Mentzelia pectinata* is clinal. In the northwest portion of the range the individuals have small yellow flowers (petals 8–14 mm long) with retuse petal tips and large seeds (1.4 mm long and 1.2 mm wide), 20–25 seeds per capsule. In the southwest section of the range the other extreme of the cline has larger flowers with deep orange petals (12–20 mm long) with mucronate tips and small seeds (1.2 mm long and 1.0 mm wide), 30–38 seeds per capsule. In the northwest the populations are generally associated with *Quercus lobata* and occur on fine, white shale soils. To the southeast the populations occur on heavier brown clay soils mainly in grassland communities. Most populations are intermediate representing various combinations of the morphological extremes, and in general occur on the finer white or light gray soils. In intermediate populations with both orange and yellow flowered individuals present, it appears that the orange flowered plants are abundant only in years of adequate rainfall, more scarce in drier years, and completely absent in years of extreme drought (Zavortink 1966, p. 75).

One example [of fluctuation in population size] is that of *M. pectinata* in which the proportions of orange to yellow flowered individuals vary in a given year depending on the yearly rainfall conditions. In May, 1963 sufficient moisture had been received in the Cammatti Valley in San Luis Obispo County to support flourishing populations of many annual and perennial species. Species of *Mentzelia*, *Amsinckia*, *Salvia*, *Clarkia*, *Delphinium*, *Lupinus*, and of other genera formed extensive populations. *Mentzelia pectinata* was present in great abundance, covering the hillsides with thousands of individuals, and the yellow flowered plants were present in a ratio of 30:1 yellow to orange flowered individuals. In May, 1964 the Cammatti Valley population was less extensive both in number of individuals and in area, with yellow flowered individuals far outnumbering orange flowered plants by 100:1. May, 1965 showed a great change in the area, with all species much reduced in number and showing evidence of drier conditions with smaller, more depauperate-appearing individuals, more widely scattered than in previous years. The population of *M. pectinata* consisted of almost all yellow flowered plants. After much searching, only 2 orange flowered individuals could be found, and the population size was drastically reduced to between 200–300 individuals, many small and with few flowers (Zavortink 1966, pp. 20–21).

We have observed the presence of orange-flowered individuals in only a single population of var. *chrysopetala*, in which yellow-flowered plants were far more numerous, conforming to Zavortink's observations.

Left for future studies are the reportedly clinal variation in morphological features and the rare occurrence of orange-flowered individuals within populations of the yellow-flowered race. It should also be noted that other species in sect. *Trachyphytum*, including *Mentzelia veatchiana* Kellogg, also have both orange and yellow-flowered phenotypes but with less clearly delineated geographic races (Brokaw 2016). Does flower color affect pollinator selection? Do the yellow-flowered and the infrequent orange-flowered plants in mixed populations interbreed? How is flower color inherited?

Neotypification of *Mentzelia pectinata*. Kellogg (1863) described *Mentzelia pectinata* based on a plant "found by Mrs. Hutchings on the mountains above Visalia." Mrs. Hutchings was Elvira (Sproat) Hutchings, the wife of James Mason Hutchings, who was prominent in exploring and promoting the Sierra Nevada, especially the Yosemite area (National Park Service 2015). No specimen of *Mentzelia* collected by Mrs. Hutchings has been located in the herbarium of the California Academy of Sciences (CAS) or elsewhere. If Kellogg deposited a specimen of *Mentzelia pectinata*, it likely was destroyed in the 1906 earthquake and fire, which ravaged most of the CAS plant collection.

The options for typification of *Mentzelia pectinata* are either to designate a neotype or to select as lectotype the illustration that accompanied Kellogg's original description. Our preference in designation of a specimen as neotype would be a collection well representative of the species made in the area where Mrs. Hutchings found the plant. Unfortunately our search of specimen records from this area (CCH2 2020) did not locate any *Mentzelia pectinata* specimens that fit these criteria. The type location is to the north of any collection known to us of *M. pectinata* in the Sierra Nevada. Although the illustration published as Figure 9 by Kellogg (1863) might serve as lectotype of *M. pectinata*, it does not illustrate in sufficient detail the features of the species that differentiate it from related species of *Mentzelia*. We therefore designate as neotype a collection that adequately represents the features of *M. pectinata* var. *pectinata*.

Mentzelia pectinata Kellogg, Proc. Calif. Acad. Sci. 3: 40. 1863. **TYPE: California**. Tulare Co.: "Found by Mrs. Hutchings on the mountains above Visalia," not dated (holotype, CAS?; specimen not located, probably destroyed in the 1906 San Francisco earthquake and fire). **Neotype** (here designated): **California.** San Luis Obispo Co.: Panorama Hills, near the Temblor Range, Carrizo Plain, on loose open soil with *Caulanthus*, annual, petals deep orange

with coppery base, 762 m, [35.182190°, -119.721648°], 27 Mar 1965, *D. Wilken 130* (OBI132149; isoneotypes, CSLA005776, UCR0037482).

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GUTIÉRREZ OF *GUTIERREZIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Mariano La Gasca y Segura, known as Lagasca, named a southwestern North American plant *Gutierrezia* without recording who he was honoring. The association of Lagasca with Pedro Gutiérrez Bueno, a leading chemist and pharmacist in Madrid at the same time that LaGasca was director of the Royal Botanical Garden there, makes it likely that Gutiérrez Bueno was the intended honoree.

The genus *Gutierrezia* was clearly named for Gutiérrez, but who was Gutierrez? Nesom in *The Flora of North America* (2006) wrote "Possibly for Pedro Gutierrez, Spanish nobleman, not specified by Lagasca." Fernald (1970) wrote "Named in 1816 for Pedro Gutierrez, correspondent of the botanical garden in Madrid." Seeking dates for the life of Pedro Gutierrez, I found Pedro Gutiérrez Bueno (1745-1826), who seems likely as the person honored by Lagasca.

Gutiérrez Bueno was a well-known apothecary, chemist, and pharmacist in Madrid. Born April 28, 1743, at Cáceres, he studied at the Royal Studios of San Isidro (*Los Reales Estudios de San Isidro*) and was admitted to the Royal College of Apothecaries in Madrid. He opened an apothecary shop there in 1777. In 1785, he was appointed professor of chemistry at San Carlos College of Surgery in Madrid and in 1787 received an appointment to the Museum of Natural History (*el Real Gabinete de Historia Natural*). In these roles he recognized the need for better textbooks and so wrote them. The first edition (in 1782) of his book, *Un Curso de química, teórico y práctica, para la enseñanza del Real Laboratorio de Química de esta Corte*, taught the traditional view of chemistry, in particular that phlogiston was responsible for burning and rusting. The new edition of his textbook (in 1788) taught Lavoisier's theory of oxidation, using new terms such as oxygen and hydrogen. In addition, Gutiérrez Bueno translated the latest French papers and incorporated their ideas into Spanish chemistry at least two years before those works were available elsewhere in Europe.

In 1792 Gutiérrez Bueno was appointed the chief apothecary of His Majesty Charles VI, which gave him intellectual control of how chemistry was taught at the Ministry of State, one of the three major laboratories in Spain. His prestige — he was probably the most eminent chemist in Spain in the last decade of the 18th century — and his much-reissued books led to rapid support of modern chemical ideas in Spain.

These conceptual changes were denounced by phlogiston supporters, led by Gutiérrez Bueno's former mentor, José Viera y Clavijo (1731-1813), with the result that all three major chemistry laboratories were closed. They reopened as the Royal Laboratory of Madrid in 1799 under Joseph Louis Proust (1754-1826) with a modern curriculum.

Despite the upheaval, Gutiérrez Bueno retained his chair in chemistry in the College of Surgery at San Carlos and in 1804 became director and professor of the newly created College of Pharmacy of Madrid. He retired in 1815 and died in Madrid on May 11, 1822.

Gutiérrez Bueno's writings ranged from studies of the production of gunpowder to dye manufacture. Generally, his papers incorporated information on the chemical composition of the materials and the chemical processes involved, whether the source was mineral or vegetable (inorganic

or organic in our terminology), and ranged from applied science to medicine. In the history of Spanish chemistry, he is central to the modernization of chemistry and remarkable for so quickly changing his views to embrace modern chemistry.

The namer of the genus *Gutierrezia*, Mariano La Gasca y Segura (1776-1839), known as Lagasca, studied medicine in Zaragoza and botany in Valencia. After moving to Madrid in 1800, he studied botany and medicine with Antonio José Cavanilles (1745-1804), a well-known botanist and physician. Lagasca became a professor at the University of Madrid and was a vice-director of the Royal Botanic Garden in Madrid under Cavanilles. In 1807 he was appointed director of the Royal Botanical Garden (TheBiography 2018). He named *Gutierrezia* in 1816 from a specimen collected by the Sessé and Mociño expedition in 1787-1803 in Nova Hispania (Mexico into the southern USA) (Schneider 2019; JSTOR).

I cannot directly link Lagasca to Gutiérrez Bueno. However, in the first two decades of the 19th century both men were leading members of the scientific community in Madrid. Gutiérrez Bueno was an apothecary, pharmacist, and chemist. Lagasca was a physician and botanist. Lagasca's publication appeared in 1816, the year after Gutiérrez Bueno's retirement. Lagasca did not specify the Gutiérrez for whom he named the plant: it may have been too obvious.

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AYENIA COMPACTA AND *AYENIA FILIFORMIS* (MALVACEAE) IN THE WHITE TANK MOUNTAINS OF THE ARIZONA SONORAN DESERT

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ABSTRACT

Two species of *Ayenia*, *A. compacta* and *A. filformis*, are represented in the White Tank Mountains (WTM) of Arizona. However, the confused taxonomic history of Sonoran Desert *Ayenia* and the absence of easily identifiable traits in the literature makes the distinction between them uncertain. This paper details traits that can be used to distinguish them in the field and concludes that they are separate species growing sympatrically in the WTM.

Two species of the genus *Ayenia* appear to be present in the White Tank Mountains (WTM) in the Sonoran Desert west of Phoenix, Arizona. Identification of which species are present, however, is complicated by the confusing and inconsistent taxonomic history of *Ayenia* in the area.

Ayenia is a New World genus consisting of about 80 species distributed from Argentina north through the tropics to the southern USA, with representatives also in some Caribbean islands. Four *Ayenia* species are recognized in Arizona (Dorr 2015): *A. compacta*, *A. filiformis*, *A. jaliscana*, and *A. microphylla*. *Ayenia jaliscana* and *A. microphylla* are found in Arizona to the south and east of the WTM but have not as yet been identified in the WTM. These two species have readily recognizable distinguishing traits (Dorr 2015) and will not be addressed in this paper.

Cristóbal's revision of *Ayenia* (1960) followed a scheme whereby three sections of *Ayenia* species were defined primarily according to differences in the plant petals. In this scheme, *A. compacta* and *A. filiformis* were grouped in one section and *A. jaliscana* and *A. microphylla* were assigned individually to two other sections.

Among the defining differences between Cristóbal's three sections are features of the petal laminas: *Ayenia compacta* and *A. filiformis* laminas have elongated clefts beginning medially on their distal edges and cutting centrally for about one-third to one-half the length of the lamina; *A. jaliscana* and *A. microphylla* do not have these clefts. Second, on the petal lamina outer surfaces, at the proximal ends of the clefts, *A. compacta* and *A. filiformis* have worm-like structures called appendages, whereas *A. jaliscana* and *A. microphylla* do not. Finally, Cristóbal (1960, pp. 158–159) noted that the petal lamina shapes differ between species, with other character differences consistently accompanying specific shapes. In the two WTM *Ayenia*s, clefts and appendages are present on the laminas and differences in lamina shapes are accompanied by other specific differences. So it would seem they are *A. compacta* and *A. filiformis* (Figs. 5–7, 10–15), but uncertainty persists in distinguishing one from the other.

The taxonomic history of *Ayenia compacta* and *A. filiformis* has been and continues to be complicated. Since Watson's description of the type specimen of *A. filiformis* in 1889 and Rose's 1905 description *of A. compacta*, the two entities have variously been called *A. filiformis* (Watson 1889), *A. microphylla* (Palmer 1890; see Rose 1905), *A. compacta* (Rose 1905), *A. wrightii* (Standley 1920), *A. pusilla* (Standley 1920), and *A. californica* (Jepson 1925). Cristóbal's revision put *A. compacta, A. filiformis,* and *A. microphylla* in Arizona and relegated *A. pusilla* (which had become something of a generic basket for North American species) to northern South America. *Ayenia pusilla* nevertheless

continued to appear in North American flora for several more years (Shreve & Williams 1964; Keil 1973). Cristóbal restricted *A. wrightii* to central Mexico.

More recently, *Ayenia insulicola*, a species Cristóbal (1960) and Dorr (pers. comm., 2019) restrict to the Caribbean, has appeared in herbaria identifications (e.g. Arizona State University, Phoenix Desert Botanical Gardens, University of Arizona, Utah State University) as one of the species names used to replace *pusilla* (Ayers pers. comm., 2019) but how it was determined that *A. insulicola* is a southwestern species is not clear and the reasoning apparently has not been published. It seems unlikely that a genus which demonstrates a considerable ability to evolve and includes a species (*A. insulicola*) which is at home at sea-level in the humid Caribbean environment, would also have the same species existing at an altitude of 1000-3000 feet in the Sonoran Desert, a few thousand miles away.

One last complication has been presented by Felger (2000, 2015), who questioned whether *Ayenia compacta* and *A. filiformis* are really separate species. This question is addressed by the information presented below.

For clarity, I will use the names *A. compacta* and *A. filiformis* throughout the paper, applying them as seems appropriate to the final conclusion.

Material and methods

The 25 WTM plants discussed in this paper were found entirely in washes that are eroding into bajadas on the east side of the mountains. Previous researchers have found other plants on slopes outside of washes and somewhat higher in the mountains (e.g., Keil 1973) but the searches performed for this paper were restricted to washes to prevent soil damage from repeated visits as much as possible. The west side of the mountains have not been searched. All of the plants found were growing in washes at the base of and closely approximated to or from under small to mid-sized (ca. 50x50 cm) rocks; most grew on the downstream sides of their rocks. Healthy plants grew as tall as 40 cm, but many were heavily browsed. Seasonal and weather variations significantly affected the growth and health of the plants over the 3 years they were observed, with a few not surviving the summer heat. Flash floods washed away some plants but also presumably distributed seeds.

Four plants with deep red or purple flowers (*Ayenia filiformis*) were found in three different washes separated by several miles, while 19 plants with yellow/orange flowers and/or distinctive fruit (*A. compacta*) were all found scattered over about 0.5 mile in a single wash, with one of the purple-flowered plants growing among them. Two plants in the same wash, lacking flowers and fruit, were not identified beyond genus.

The following descriptions contrast *Ayenia compacta* and *A. filiformis* in WTM and combine my visual observations with information gleaned from my photographs of the 0.1–4 mm structures on the plants.

Results and conclusions

Overall descriptions of the plants are available in other publications (e.g., Lawrence 1929; Cristóbal 1960; Dorr 2015) so my comments are restricted primarily to diagnostic differences in flowers and fruit, except to note that (a) *Ayenia compacta* branches may be decumbent or erect while *A. filiformis* has an erect branching pattern (Cristóbal 1960) (Figs. 1, 2); (b) *A. compacta* basal leaves are ovate, about 1 cm long, with minimal or no pubescence, while *A. filiformis* basal leaves are ovate and may be small but also may be 2–3 cm long and may or may not retain pubescence; and (c) terminal leaves in both species are 1–3 cm long and either ovate-lanceolate or linear, with those of *A. filiformis* in general being noticeably more pubescent than *A. compacta* (Figs. 3, 4). These branch and leaf traits

may be suggestive but are so variable between plants that their appearance in an individual plant should probably be considered as supportive rather than definitive diagnostic evidence.

Flowers of both species are beautiful and extraordinarily complex, with the most notable features including androgynophores, five stamens alternating with five staminodes, petals composed of filamentous claws and diagnostically-shaped laminas that curve medially to attach to the staminodes (thereby "hiding" the anthers inside the flower), and the appendages (Figs. 5–7, 10–14).

The mature fruit (schizocarp) of *Ayenia* in the WTM is nearly spherical and 4–5 mm in diameter at maturity, with 5 well-defined mericarps, each containing a single seed. It bears evenly spaced spines (variously called *aculeolos*, glands, papillae, prickles, processes, spines) that are 0.3–1.3 mm long and may or may not be pubescent (Figs. 8, 9, 16).

The following traits are found together as a unit in the plants of each presumed species in the WTM.

Flowers:
1. Color: The flower color of *A. compacta* does not seem to have been previously described but may be the best distinguishing trait between the two species. *Ayenia compacta* flowers are pink, yellow, or orange-red, not deep red or purple; those of *A. filiformis* are deep red or purple, with occasional petal laminas being purple centrally and white peripherally.
2. Petal lamina shape: *A. compacta* diamond, *A. filiformis* triangular
3. Petal lamina-claw junction: *A. compacta* 135 °, with lamina attenuate on claw; *A. filiformis* 90 ° and squared-off
4. Petal lamina appendages: *A. compacta* proximal 2/3 is the color of the lamina, distal 1/3 is black; the black portion is somewhat bulbous. *A. filiformis* is 90-100 % black and is sickle-shaped.
5. Sepals: *A. compacta* sepals may be green but often are a mottled red, sometimes on the same plant; *A. filiformis* sepals are bright green.

Fruits:
1. Mature fruit color: *A. compacta* red (immature are green), *A. filiformis* green
2. Fruit spines – size and pubescence: *A. compacta* <0.7 mm, with very short or absent hairs; *A. filiformis* 0.5-1.3 mm, with long, easily visible hairs
3. Fruit spines – color: *A. compacta* dark brown to black (even when fruit is green), *A. filiformis* green

This consistent combination of traits in plants of yellow/orange (*Ayenia compacta*) vs. purple (*A. filiformis*) flowers defines the two species. Naming the purple-flowered plants *A. filiformis* follows the original description of Watson (1889), who described the type, found in Sonora, Mexico, as "petals purple" and "fruit … beset with numerous slender green processes." Descriptions of *A. compacta* do not include the yellow/orange flower color except as "brownish" (Jepson 1925; Adams 1951) but do mention "short brown papillae" on the fruit (Rose 1905) and "capsule… muricate with black glands" (Adams 1951). Jepson (1925) noted that the type specimen of *A. californica*, now synonymized with *A. compacta*, was found "on the western edge of the Colorado desert"; photos of *A. compacta* from Anza-Borrego State Park and the surrounding desert in Southern California all show plants that are apparently the same as the plants with yellow/orange flowers in the WTM (e.g., CalFlora, SEINet websites).

These descriptions are of live plants in the field. In herbarium specimens, changes in color, shape, and other parameters in the plants' minute structures due to drying, aging, and mounting create considerable impediments to their proper identification, though close examination may help to suggest which species they are. As though in confirmation of the difficulties of identifying older herbaria specimens, many such specimens in Arizona herbaria have over the years been renamed *Ayenia*

filiformis (and *A. insulicola*, as noted above) from *A. pusilla*, seemingly without regard to the possibility that *A. compacta* could be present.

Despite the uncertain identification of some herbarium specimens, it appears that *Ayenia compacta* is a species primarily of the lower Colorado desert, growing on both sides of the Colorado River and west into California and south into Baja California. Its easternmost distribution ends probably very near the WTM. *Ayenia filiformis*, on the other hand, occurs as far east as Texas but may have its westernmost distribution also ending near the WTM, though a small number have been identified in western Arizona. The two species meet and grow together in the WTM.

In summary, there are 2 species of *Ayenia* in the WTM (*Ayenia compacta* and *A. filiformis*), readily distinguished from each other by differences in flower color, petal lamina shape, petal appendage color and shape, and by the differences in fruit color and in the length, color, and pubescence of the fruits' spines, with supplemental support by other traits as described above and in the figures.

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Figures

Figure 1. *Ayenia compacta*. Features visible on the plant that may assist in identification are erect, decumbent, and procumbent branches; linear and lanceolate terminal leaves; small ovate basal leaves; numerous fruits turning from green to red; and orange flowers.

Figure 2. *Ayenia filiformis*. Visible are erect branches; linear and lanceolate terminal leaves, large ovate basal leaves, green fruit, and deep red/purple flowers.

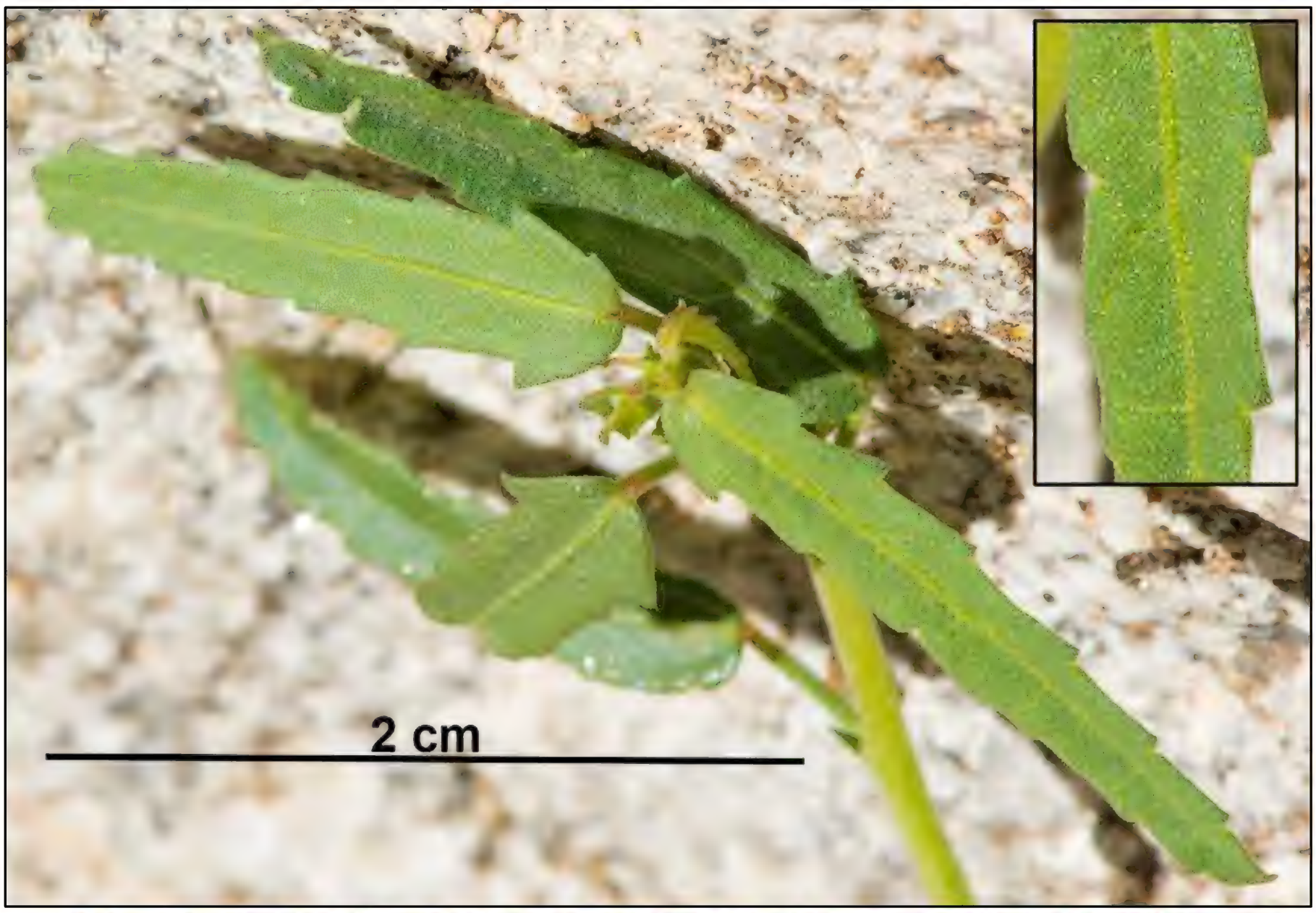

Figure 3. *Ayenia compacta*. A. Linear and lanceolate terminal leaves. Inset: lightly pubescent terminal leaf. B. Glabrous small ovate basal leaves plus ripening fruit.

Figure 4. *Ayenia filiformis*. A. Pubescent linear terminal leaves and one mature flower. Inset: pubescent terminal leaf. B. Pubescent small ovate basal leaves and ripening fruit.

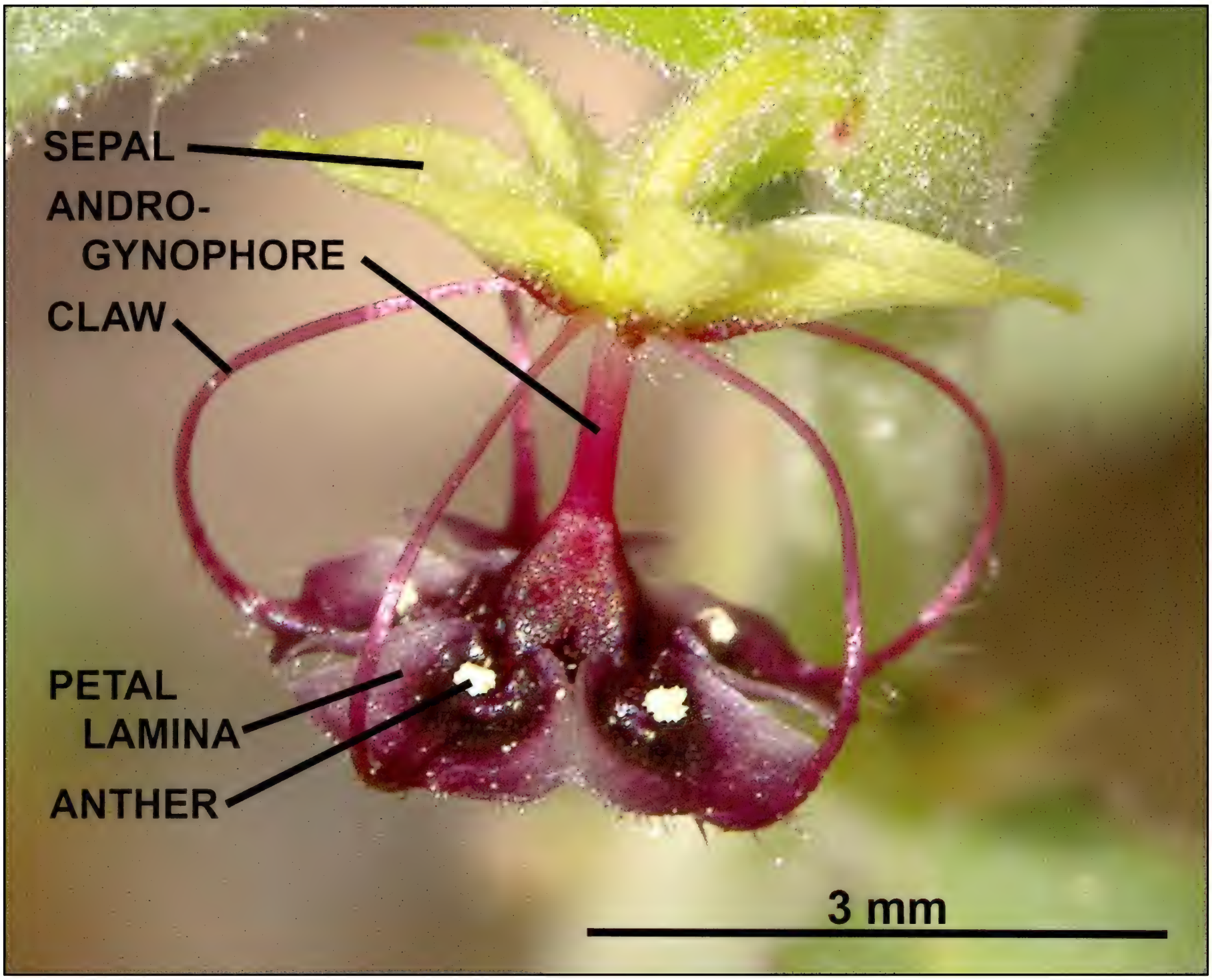

Figure 5. *Ayenia filiformis*. Flower, lateral view, annotated. Anthers on undersurface of laminas at proximal ends of clefts.

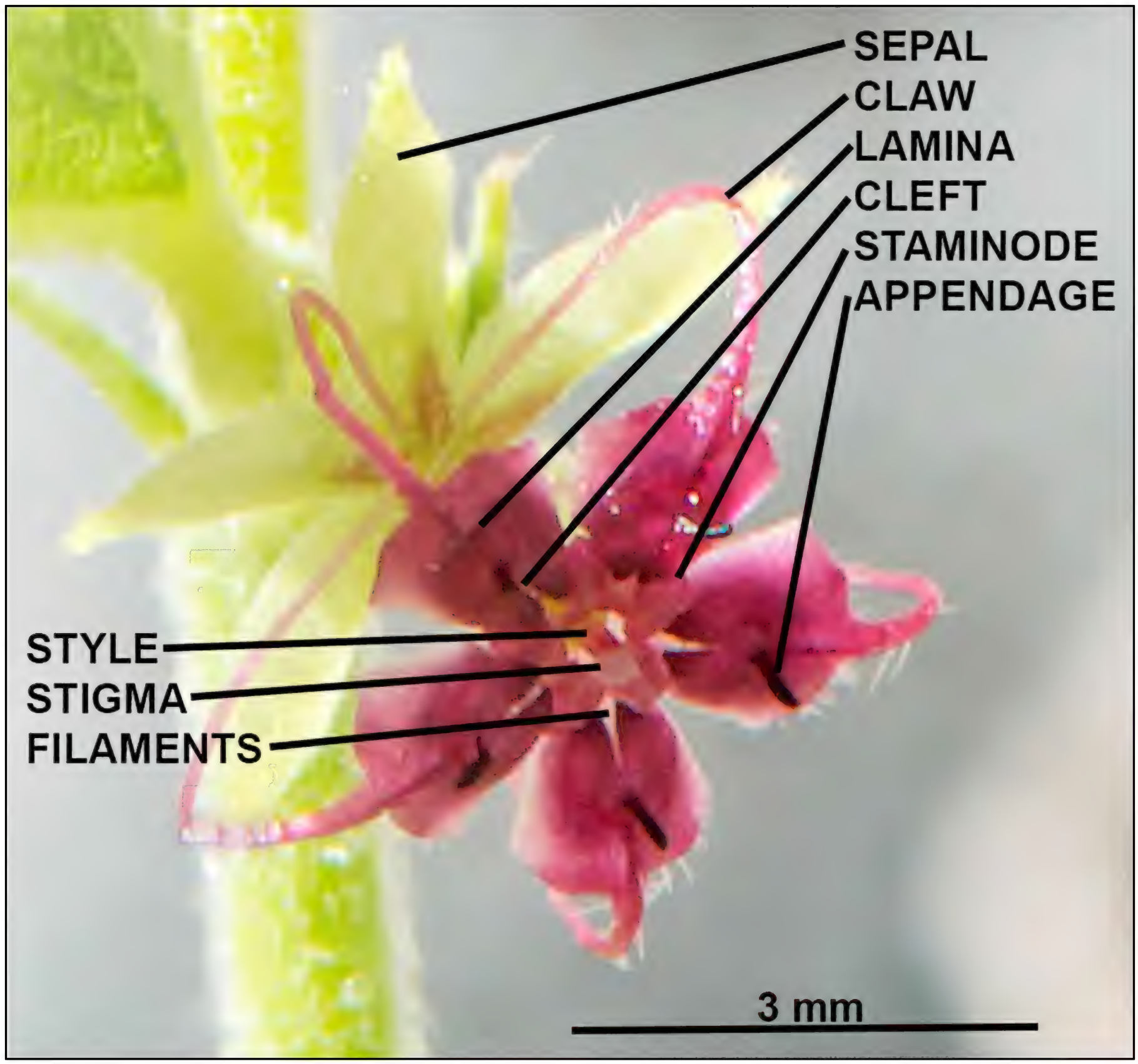

Figure 6. *Ayenia filiformis*. Flower, distal end view, annotated. Lamina attachments to staminodes visible.

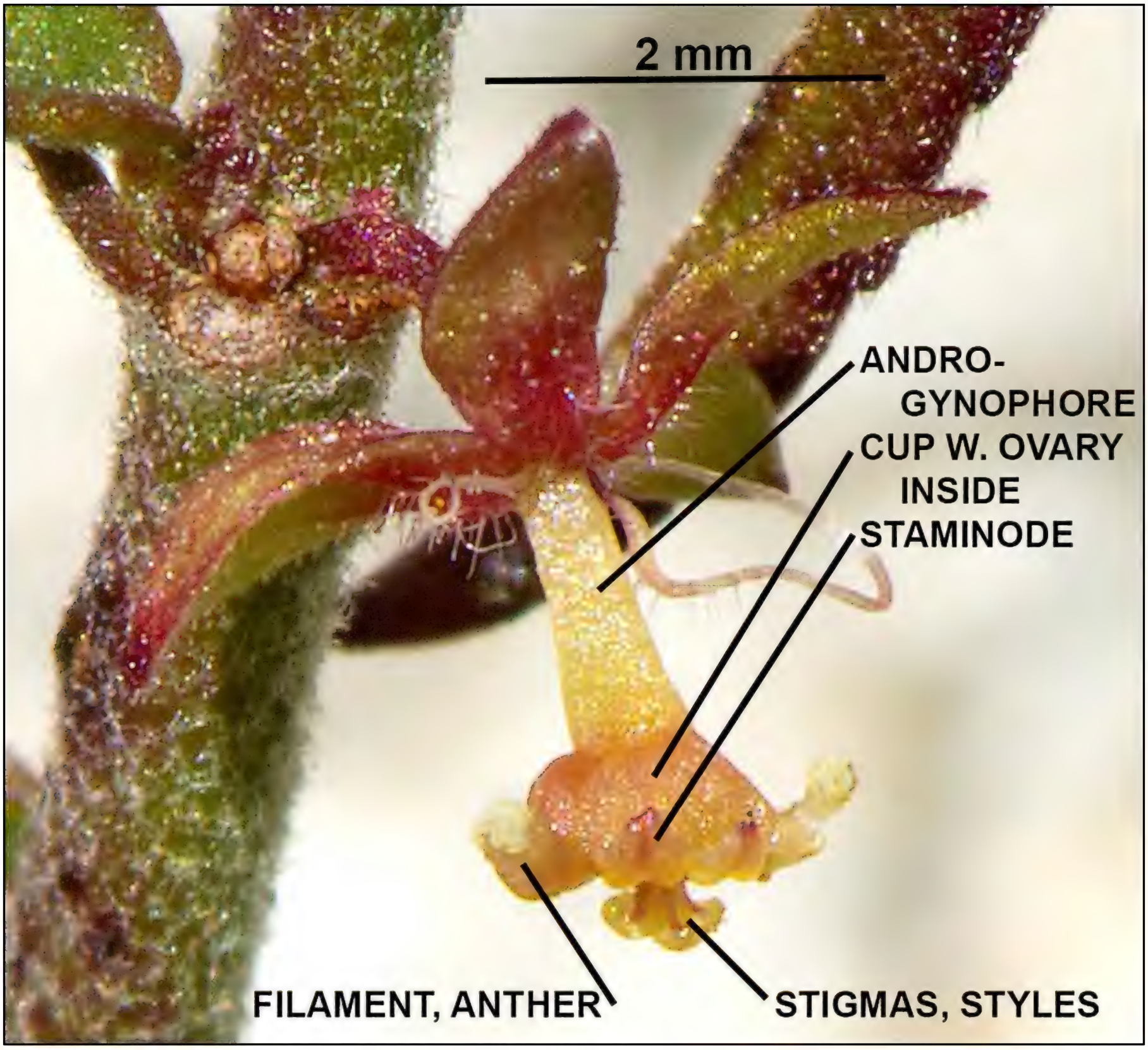

Figure 7. *Ayenia compacta*. Damaged flower with missing petals, exposing details of red sepals, androgynophore, pistils, and stamens.

Figure 8. *Ayenia compacta.* A. Immature green fruit with small dark brown spines having a few dark hairs. B. Mature red fruit with small dark spines having a few short hairs.

Figure 9. *Ayenia filiformis*. A. Green fruit with pubescent long green spines. One fruit has orange color on side facing sun. B. Green fruit with spine traits as in 9A. C. Reddish fruit turning brown (ripe seeds); note pubescent green spines.

Figure 10. *Ayenia compacta*. Flower lateral view.

Figure 11. *Ayenia compacta*. Flower distal (end) view. Note diamond-shaped lamina attenuate on claw and the clear view of the laminas attaching to the staminodes.

Figure 12. *Ayenia filiformis.* Flower lateral view.

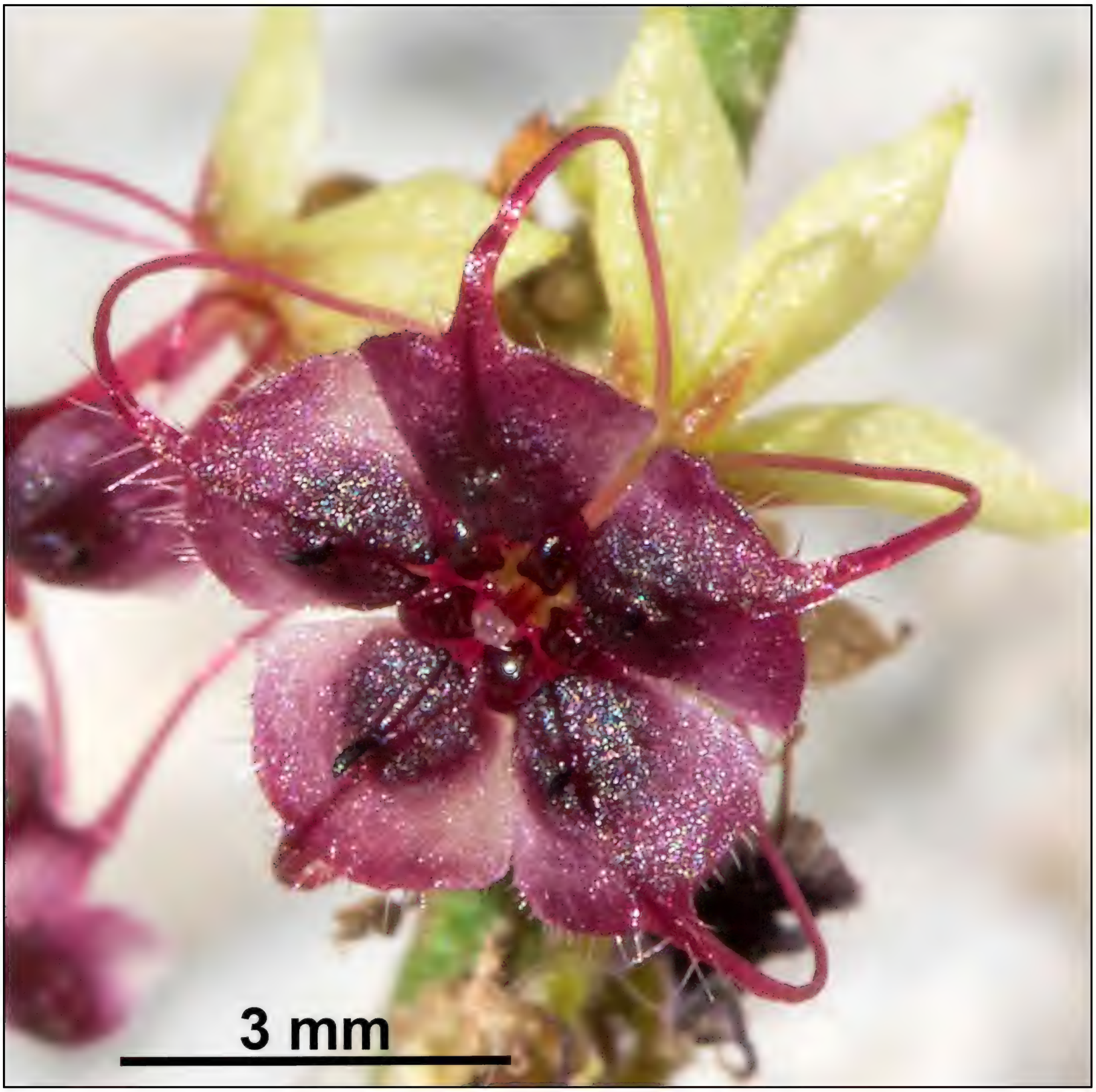

Figure 13. *Ayenia filiformis.* Flower distal (end) view. Note trapezoidal shape of lamina joining claw at a 90˚ angle and the clear view of the laminas attaching to the staminodes.

Figure 14. *Ayenia compacta*. Flower with 1 petal lamina attached to the undersurface of a sepal, one lamina just breaking away, one petal swinging freely, and one attached to staminodes. The petal lamina attaches to the staminodes and simultaneously attaches by means of its cleft to the stamen filaments, leaving the anther exposed on the lamina undersurface and the appendage on the external surface.

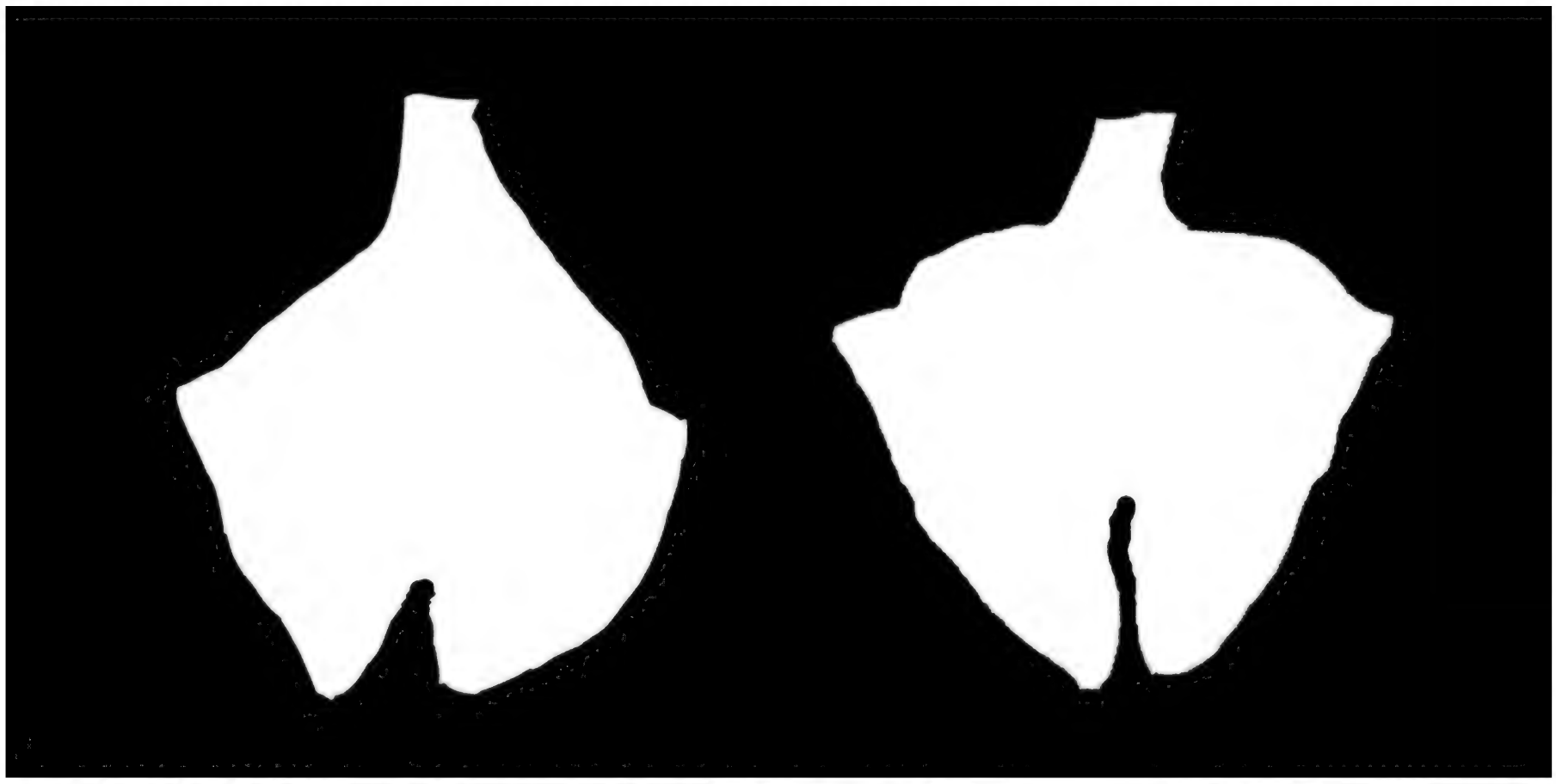

Figure 15. Petal lamina outlines. Left: *Ayenia compacta.* Right: *Ayenia filiformis*.

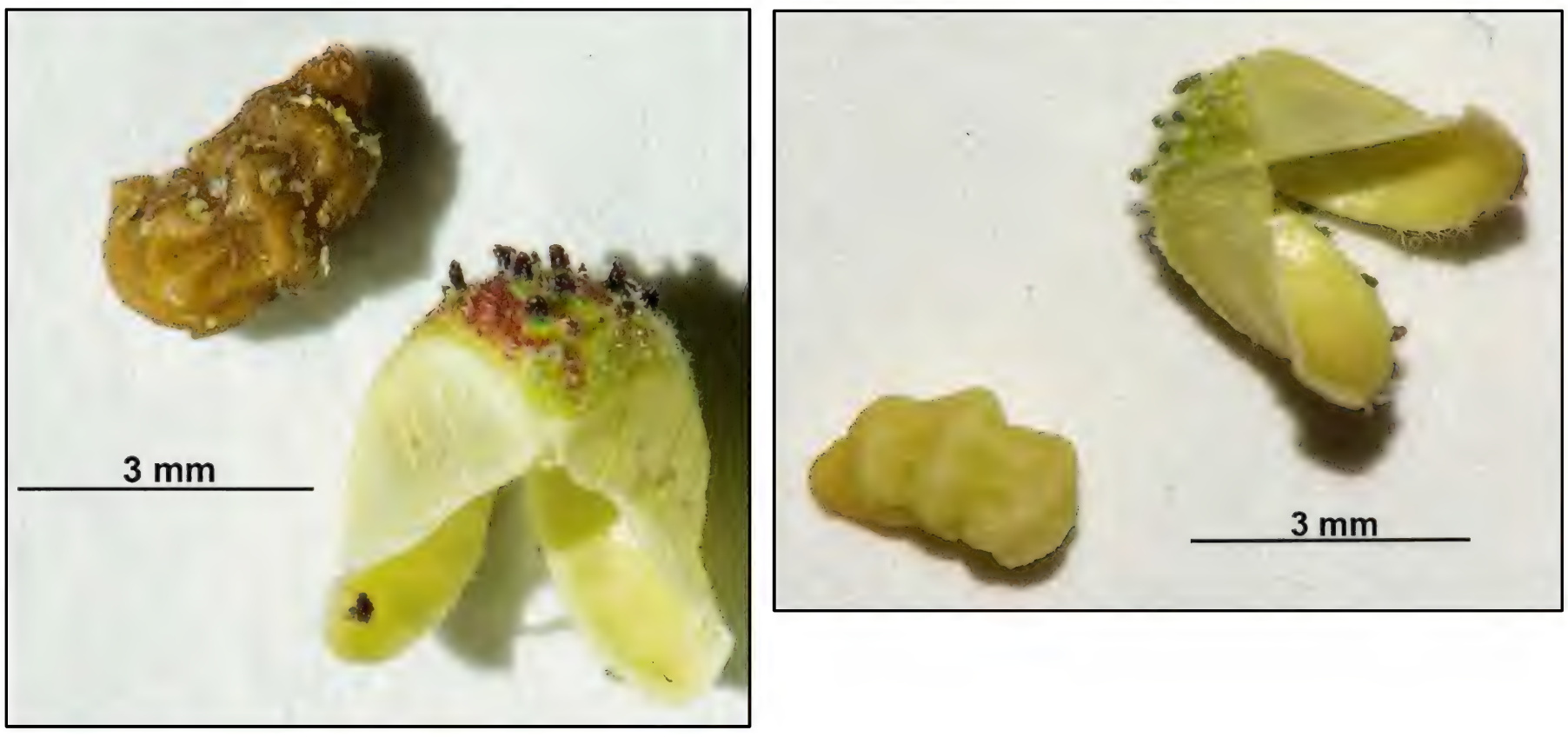

Figure 16. Seed and mericarp. Left: *Ayenia compacta.* Right: *Ayenia filiformis.* Note the nearly identical seed shapes and patterns of "wrinkles" on the seed surfaces. Note also the differences in color of the mericarp spines.

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NOTES ON *THAMNOSMA TEXANA* (RUTACEAE) WITH THE DESCRIPTION OF A NEW VARIETY

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ABSTRACT

A lectotype is provided for *Thamnosma texana* (A. Gray) Torrey, **Thamnosma texana** (A. Gray) Torrey var. **purpurea** (Woot. & Standl.) L. Woodruff, **comb. et stat. nov.**, formally recognizes a geographical variant, and intergradation in the two varieties of *T. texana* is discussed.

Thamnosma (Rutaceae) is one of only a few genera of herbaceous plants (e.g. *Menodora*, *Selinocarpus*) whose distribution is disjunct between North America and Africa/southwest Asia (Thiv et al. 2011). Five species occur in North America: *T. montana* Torr. & Fremont and *T. texana* (A. Gray) Torrey (southwestern USA and Mexico), *T. pailensis* M.C. Johnst. and *T. stanfordii* I.M. Johnst. (northeastern Mexico), and *T. trifoliata* I.M. Johnst. (Baja California Sur).

In preparing a taxonomic treatment of *Thamnosma* for the forthcoming Volume 13 of Flora of North America North of Mexico, several details are attended to here. A lectotype is provided for *Thamnosma texana*, a name for a geographical variety of *T. texana* is formalized as a new combination, and intergradation between varieties of *T. texana* is discussed.

Thamnosma texana (A. Gray) Torrey in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 42. 1859 (as texanum). *Rutosma texana* A. Gray, Gen. Amer. Bor. 2: 143, pl. 155. 1849. **LECTOTYPE** (designated here): **USA**. **Texas**. Without specific locality, without date, *C. Wright s.n.* (GH 00044214!; isolectotypes: GH 00044215!, NY 3787945!, NY 3787946!).

Asa Gray mentioned three collections in his protologue for *Rutosma texana*: those of Mr. Lindheimer, Mr. Wright, and Dr. Gregg. Although Lindheimer's collection was acknowledged for the illustration plate, Wright's material has "nov. gen." (or "n. g.") written on the label in Gray's handwriting. The Wright specimen kept by Gray in his herbarium is selected here as lectotype. Isolectotypes include a specimen ex herb. John A. Lowell transferred from the Boston Society of Natural History to GH in 1941 and two specimens at NY. Although not on Gray's label, the GH database gives 1848 as the year of collection (GH Specimen Database 2013).

Geographical variation in *Thamnosma texana*

A yellow-flowered entity is found generally east of the 100th Meridian in the Edwards Plateau of central Texas and to slightly farther west in the Rio Grande valley at 50–500 m. Its range extends south to the Mexican states of Coahuila, Nuevo León, and Tamaulipas at elevations to 2500 m. The Edwards Plateau is a grassland with stands of scattered to dense oak and juniper, along with many other woody species, and underlain by shallow, limestone- or granite-derived, well-drained soil. Further south near the Texas-Mexico border, pockets of tall, dense Tamaulipan thorn scrub vegetation are habitat for var. *texana* (see Correll & Johnston 1970 for further description of the vegetation of these areas).

Figure 1. *Thamnosma texana* var. *purpurea*, Big Bend National Park. Photo by Roy Morey.

Figure 2. *Thamnosma texana* var. *texana*, central or south Texas. Photo by Steven Schwartzman.

Figure 3. *Thamnosma texan*a, intergrading varieties. Open circles are var. *texana*; closed circles are var. *purpurea*.

Plants with maroon-tinged flowers have a wider distribution and occur west of the 100th Meridian in Texas to New Mexico and mostly southeastern Arizona (western Arizona documented in Anderson & Francois 2013) at 300–1700 m. The area falls largely within the Chihuahuan Desert. In Mexico, *Thamnosma texana* var. *purpurea* occurs in Chihuahua, Coahuila, Durango, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Sonora, and Zacatecas at elevations up to 2000 m. A chromosome count of n = 9 was made for var. *purpurea* (Ward 1984). Only one other count from another species of *Thamnosma* has been reported, *T. montana* with n = 10 (Parfitt et al. 1990).

No other character differences other than flower color could be found (Figs. 1, 2), but the two taxa are separated geographically (Fig. 3). Both color forms have been observed together at a site near (aptly named) Junction, Texas.

Thamnosma texana (A. Gray) Torrey var. **purpurea** (Woot. & Standl.) L. Woodruff, **comb. et stat. nov**. *Rutosma purpurea* Woot. & Standl., Contr. U.S. Natl. Herb. 16(4): 143. 1913 (as purpureum). *Thamnosma texana* f. *purpurea* (Woot. & Standl.) Lundell, Amer. Midl. Naturalist 29: 475. 1943. **TYPE: USA. New Mexico**. Doña Ana Co.: Bishops Cap at the S end of the Organ Mountains, 4 Apr 1903, *E.O. Wooton s.n.* (holotype: US 00101542! [old US #560630]; isotypes: ARIZ-2 sheets!, CAS 0006015!, CAS 213696!, MIN 1002245 (image, JSTOR 2020), RM 0003823 (image, JSTOR 2020), TEX 00371479!, UC!, US 00101542!).

Thamnosma aldrichii Tharp, Amer. Midl. Naturalist 33: 667. 1945. **TYPE**: **USA**. **Texas**. Pecos Co.: 6 Jun 1943, *B.C. Tharp 43990* (holotype: TEX!; isotypes: CAS!, GH!, MO!, NY!, TEX!, US!).

The two varieties are distinguished as follows:

1. Petals yellow throughout ..... **Thamnosma texana** var. **texana**
1. Petals creamy white with a broad maroon area (may be variable) on adaxial surface ..... **Thamnosma texana** var. **purpurea**

Both varieties are among the earliest spring flowers (February–March) in the region and each may continue to flower sporadically throughout the year after rains.

Representative specimens. Although many other collections exist, one specimen from each state is listed as reference. The author has seen material of all of the specimens cited, but the presence of duplicates in some herbaria is based on online databases including SEINet (2020) and UNAM (2018). The author has seen no material from Durango, but Villaseñor (2016) lists the species from that state.

Thamnosma texana var. ***texana***. **USA**. **Texas**. Kinney Co.: Hwy 277, 8.7 mi SE of Kinney Co. line, 1.8 mi NW of Maverick Co. line, 19 Mar 1983, *Barnett & Dorr 83039* (MEXU, MO, TEX). **MEXICO**. **Coahuila**. Sierra de La Rata, 27°05'–27°03' N, 101°02'–101°05' W, 550–1700 m, 14 Mar 1973, *Johnston et al. 10170A* (TEX). **Nuevo León**. Mpio. Rayones: Santa Rosa -> Ciénega del Toro, 1400 m, 19 Feb 1992, *Hinton et al. 21785* (MO, TEX). **Tamaulipas**. 6 mi N of Santander Jiménez, 800 ft, 9 Dec 1959, *Johnston 4898* (LL, TEX).

Thamnosma texana var. ***purpurea***. **USA**. **Arizona**. Pima Co.: Coronado National Forest, on Forest Rte 371 (Redington Rd), ca. 3 mi E of National Forest boundary, 32°15'36" N, 110°39'12" W, 1100–1300 m, 13 Apr 1998, *Schmidt et al. 2643* (ARIZ, MO, TEX). **New Mexico**. Doña Ana Co.: NE Robledo Mtn, 11 mi NW of Las Cruces, 5100 ft, 23 Apr 1983, *Ward & Soreng 83-019*, **n=9II** (NMC, NY, TEX). **Texas**. Val Verde Co.: Devil's River, Dolan Falls, Nature Conservancy Property, 29°53.07' N, 100°59.37' W, 10 Mar 2003, *Simpson 10-III-03-6* (TEX). **MEXICO**. **Chihuahua**. N end of E side of Sierra del Cuchillo Parado, 29°37' N, 104°55' W, 1000–1300 m, 21 Oct 1972, *Wendt et al. 9789* (CAS, NY, TEX). **Coahuila**. La Favorita Ranch on N slope of the Cañón Bonanza, SE end of Sierra de la Purísima, 26°25'–26°26' N, 101°30'–101°28' W, 1300–1650 m, 19 Mar 1973, *Johnston et al. 10293* (CAS, F, MO, NY, TEX). **Hidalgo**. Mpio. Actopan, El Capulín, near km 134 on hwy between Actopan and Ixmiquilpan, ca. 1800 m, 4 Aug 1948, *Moore & Wood 4252* (A, MEXU). **Nuevo León**. Mpio. Galeana, S of Rancho Aguililla, 2000 m, 8 Jul 2000, *Hinton et al. 27626* (MO, TEX). **Querétaro**. Mpio. Cadereyta de Montes, 15 km al N de Cadereyta, alrededores de Corral Blanco, 2000 m, 31 Jul 1990, *Rzedowski 49624* (MEXU). **San Luis Potosí**. Minas de San Rafael, Nov 1910, *Purpus 4835* (F, MO, UC, US). **Sonora**. Mpio. Agua Prieta, flats N of airstrip N of Rancho La Calera, NE of Sierra Anibacacachi, ca. 7 km (by air) SW of Agua Prieta, 31°14'57" N, 109°37'01" W, 1256 m, 24 Apr 2004, *Van Devender et al. 2004-335* (ASU, TEX, USON). **Zacatecas**. 18 mi SW from Cedros turnoff at Estación Margarita, 1 Aug 1975, *Engard & Gentry 679* (ASU, DES, LL).

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A MULTIVARIATE MORPHOMETRIC ANALYSIS OF *SOLIDAGO* SECT. *SOLIDAGO* AND SECT. *MULTIRADIATAE* (ASTERACEAE: ASTEREAE)

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ABSTRACT

A multivariate morphometric study of the goldenrod groups *Solidago* sect. *Solidago* and *S.* subsect. *Multiradiatae* was conducted to assess the morphological differences among *S. virgaurea* and the closely related Eurasian species, *S. dahurica*, *S. decurrens* (including *S. insularis* and *S. praeflorens*), *S. horieana*, *S. kurilensis* (including *S. nipponica*), *S. litoralis*, S. *minutissima*, *S. pacifica,* and *S. yokusaiana* and the putatively related North American species *S. macrophylla* and *S. leiocarpa*, *S. multiradiata*, and *S. spithamaea*. Analyses of a matrix of 217 specimens by 34 traits provided support for recognizing 12 species. Statistically, *S. macrophylla* was not as strongly separated from the Eurasian group of species as was the *S. multiradiata* group of three species. Some Eurasian taxa were not included in the a priori portions of the analyses. The following new combinations are proposed: **Solidago** ser. **Macrophyllae** Semple & J.B. Beck**, Solidago** sect. **Multiradiatae** (Semple) Semple & J.B. Beck*;* **Solidago decurrens** Loureiro var. **insularis** (Kitam.) Semple. A neotype is designated for *Solidago decurrens* and for *S. cantonensis*.

Solidago subsect./ser. *Solidago* includes 4 to 11 species depending upon the taxonomic treatment followed (Nesom 1993; Iwatsuki et al. 1995; Chen & Semple 2011; Sakaguchi et al. 2018; Semple 2020 frequently updated) — ***S. virgaurea*** L. (Figs. 1-2; including multiple European subspecies and varieties of uncertain status and numerous synonyms; this is the type species of the genus), ***S. litoralis*** Sav. (Figs. 3-4), ***S. dahurica*** (Kitag.) Kitag. ex Juz. (Figs. 5-6), ***S. decurrens*** Loureiro (Figs. 7-11; with numerous synonyms including *S. insularis* Kitam. and A*mphirhapis leiocarpa* Benth.), ***S. horieana*** Kadota (Fig. 12), ***S. kurilensis*** Juz. in Komarov (Figs. 13-15, including *S. nipponica* Semple), *S. minutissima* (Makino) Kitam. (Fig. 16), ***S. pacifica*** Juz. (Figs. 17-18), and ***S. yokusaiana*** Makino (Figs. 19-20). All members of ser. *Solidago* have large lower stem leaves, inflorescences that are narrow to broadly paniculiform (although most individuals in *S. kurilensis* have more corybiform inflorescences or inflorescence branches), and generally larger involucres for the genus. Inner pappus bristles are the longest and somewhat clavate. Cypselae bodies range from glabrous to densely and evenly strigulose. Details of the nomenclature of eastern Asia taxa names are presented in Table 1, which includes several new combinations and typifications.

Solidago ser. Macrophyllae Semple & J.B. Beck[1] includes one species, *Solidago macrophylla* Pursh (Figs. 21-22), which was included in subsect. *Glomeruliflorae* by Semple and Cook (2006), based on RFLP cpDNA results in Zhang (1996) and in the multivariate study of the subsection by Cook et al. (2009). Torrey and Gray (1842) included *S. macrophylla* Pursh as a synonym under *S.*

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[1] ***Solidago*** ser. ***Macrophyllae*** Semple & J.B. Beck, **ser. nov.** **TYPE**: *Solidago macrophylla* Pursh. Involucres 8-10 mm tall; lower stem leaves largest, serrate; cyselae (± linear-obconic, glabrous, 1.4–4.4 mm, glabrous; pappi 4–7.3 mm. DNA sequence data (Beck et al. in prep.) indicate that *S. macrophylla* is the sister species to ser. *Solidago.*

squarrosa Muhl. with a question mark, noting the lack of type material at the time, and were uncertain whether it should be adopted as the older name for their *S. squarrosa*. Fernald (1950) placed *S. macrophylla* (No. 7) after *S. squarrosa* (No. 6) and before *S. calcicola* Fern. (No. 8) and *S. bicolor* L. (No. 9). Cronquist (1968) keyed out *S. macrophylla* first in having very large involucres and presented it as the first species in his floristic treatment of the genus in eastern North America. *Solidago squarrosa* and *S. multiradiata* were the second and third species treated by Cronquist. *Solidago macrophylla* has large lower stem leaves, inflorescence and phyllary traits like those of subsect. *Solidago*. The involucres are large for the genus. Inner pappus bristles are the longest and somewhat clavate.

Solidago sect. *Multiradiatae* Semple & J.B. Beck[2] includes three species: *S. multiradiata* Ait. (type species; Figs. 23-24), *S. leiocarpa* DC. (Figs. 25-26), and *S. spithamaea* M.A. Curtis ex A. Gray (Figs. 27-28). Torrey and Gray (1842) treated *S. multiradiata* as *Solidago virg-aurea* var. *multiradiata* (Ait.) Torr. & Gray, noting it was most similar to *S. virgaurea* var. *cambrica* (Huds.) DC. All members of sect. *Multiradiatae* have large lower stem leaves, rounded corymbiform inflorescences or paniculiform inflorescences with rounded-corymbiform branches, and generally larger heads for the genus. Inner pappus bristles are the longest and somewhat clavate. Cypselae bodies are moderately strigulose.

The ranges of distributions of all taxa in *Solidago* ser. *Solidago* are shown in Fig. 29, including the locations of samples used in the multivariate analyses. All taxa in the series are native to Eurasia. Ranges of individual taxa vary from broad (*S. virgaurea*, *S. dahurica*, and *S. decurrens*) to very narrow (*S. horieana* and *S. minutissima*). The greatest diversity in taxa occurs in Japan. The range of distribution in eastern North America of *S. macrophylla* is shown in Fig. 30, including the locations of samples used in the multivariate analyses. The ranges of distribution of the three species of *S.* sect. *Multiradiatae* are shown in Fig. 31, including the locations of samples used in the multivariate analyses. *Solidago multiradiata* is widely distributed in western North America from northern Alaska to California and New Mexico in the mountain and across Canada to the maritime provinces of Canada; it also occurs in extreme eastern Russia. *Solidago leiocarpa* is confined to higher elevations in New England and adjacent northern New York. *Solidago spithamaea* is native to a few high elevation locations in western North Carolina.

Numerous chromosome number reports have been published for taxa in *Solidago* ser. *Solidago*, but all reports are for diploids (2*n*=9II or 2n=18): a review of the cytogeography is in preparation. All chromosome number reports for *S. macrophylla* are diploid (Cook & Semple 2008). Many chromosome number reports have been published for sect. *Multiradiatae;* a study of the cytogeography is in preparation by J.C. Semple and J.G. Chmielewski. Diploids and tetraploids (2*n*=9II or 2n=18; 2*n*=18II or 2n=36) have been reported for *S. multiradiata* (e.g., Semple & Chmielewski 1987; Morton et al. 2018). Tetraploids (2*n*=18II or 2*n*=36) have been reported for *S. leiocarpa* mostly under the synonym *S. cutleri* Fern. (Beaudry 1963; Morton 1981 as *S. multiradiata*; Morton et al. 2018). A few hexaploid chromosome counts (2*n*=27II or 2*n*=54) have been reported for *S. spithamaea* (Semple et al. 1984, 2019; Semple & Cook 2004).

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[2] ***Solidago*** sect. ***Multiradiatae*** (Semple) Semple & J.B. Beck, **comb. et stat. nov.** *Solidago* subsect. *Multiradiatae* Semple, Sida 21: 760. 2004. **TYPE**: *Solidago multiradiata* Ait. DNA sequence data (Beck et al. in prep.) indicate that the *S. multiradiata* species group is not closely related to sect. *Solidago*.

Figure 1. Large shoot of *Solidago virgaurea*, *Moore 4617* (GH) from Germany.

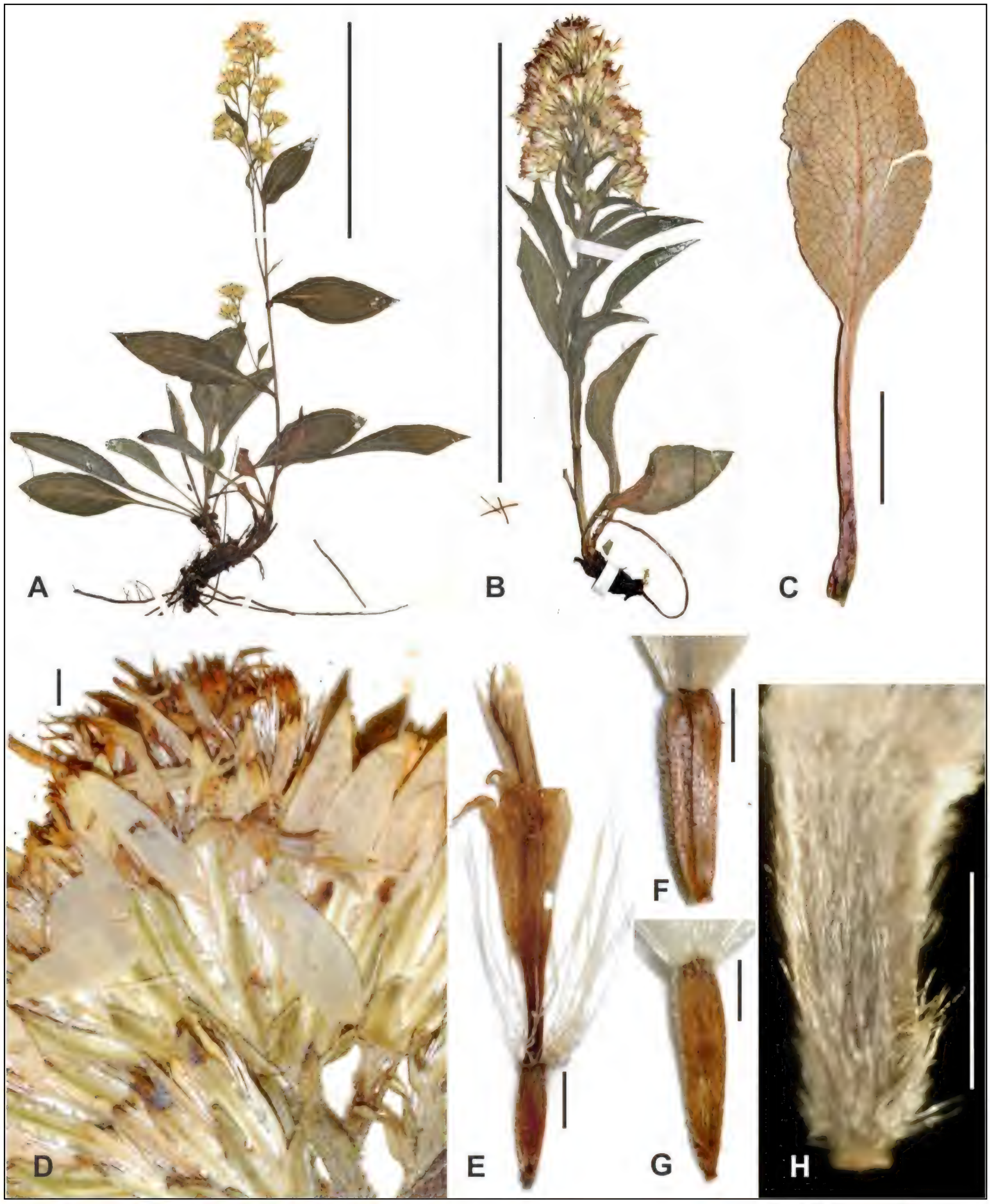

Figure 2. Details of the morphology of *Solidago virgaurea*. **A-B.** Small shoots, *Olgaard s.n.* (MO) and *Olgaard s.n.* (MO), Denmark. **C.** Lower stem leaf, *Montell s.n.* (MO), Finland. **D.** Heads, *Olgaard s.n.* (MO). **E**. Disc floret and sparsely hairy cypsela, *Moore 4617* (GH), Germany**. F-H**. Disc floret cypsela bodies, *Brandis 2846* (A) from Bosnia, *Lück s.n.* (WAT) from Hungary, and *Davis 50753* (BM) from Morocco (immature). Scale bar = 10 cm in A-B; = 1 cm in C; = 1 mm in D-H.

Figure 3. Shoots of *Solidago litoralis*, *Fiori 976* (GH) from Viareggio, Lucca Prov., Italy (right two specimens).

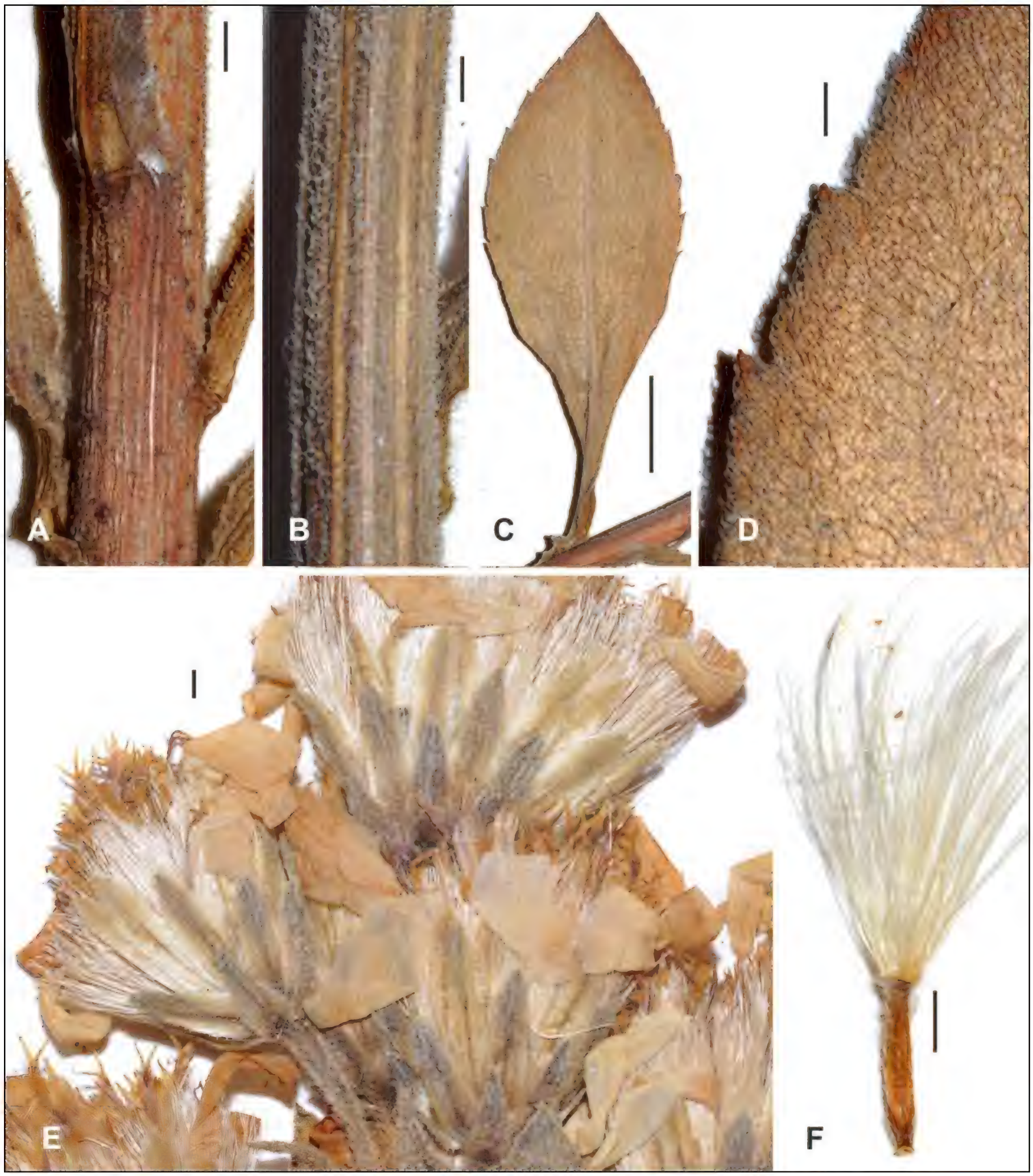

Figure 4. Details of morphology of *Solidago litoralis*. **A.** Lower stem, *Savi s.n.* (GH) . **B.** Mid stem, *Bussotti s.n.* (PI). **C-D**. Lower mid stem leaf and leaf margin, *Tomei s.n.* (PI). **D.** Heads, *Bussotti s.n.* (PI). **E.** Disc floret cysela, *Savi s.n.* (GH). Scale bars = 1 mm in A-B, D-E = 1 cm in C.

Figure 5. *Solidago dahurica*, *Brummitt & Brummitt 232* (K) from Kamchatka, eastern Russia.

Figure 6. Details of the morphology of *Solidago dahurica*. **A-B.** Lower stems, *Kramer 10953* (K) and *Stainton et al 7839* (BM). **C.** Lower stem and upper stem leaves, *Sodombekov KPL-00126* (MO). **D-E.** Upper mid stem leaf margins, *Gomolitzky s.n.* (A) and *Sodombekov KPL-00126* (MO). **F.** Stem leaf in inflorescence, *Polunin 56-102* (BM). **G.** Heads, *Brummitt & Brummitt 232* (K). **H-I.** Distally hairy disc floret cyselae, *Stainton et al. 7839* (BM). **J.** Distally more hairy disc floret cypsela body, *Abel 110* (BM) from Pakistan. Scale bars = 1 mm in A-B and G-J; = 1 cm in C-F.

Figure 7. *Solidago decurrens* var. *decurrens*, *Lin et al. 77* (A) from northeastern Taiwan.

Figure 8. Neotype of *Solidago decurrens* and holotype of A*mphirhapis leiocarpa* from Hong Kong (shoot on right *Hinds s.n.*, K).

Figure 9. *Solidago decurrens* var. *insularis*, *Koidzumi s.n.* (KYO, image provided by Shota Sakaguchi) from Amami-Oshima, Ryukyo archipelago, Japan.

Figure 10. *Solidago decurrens* var. *praeflorens*, *J. Nakai s.n.* (TI, digital image provided by Tetsuo Ohi-Toma) from Hachijyo Is., Izu archipelago, Japan.

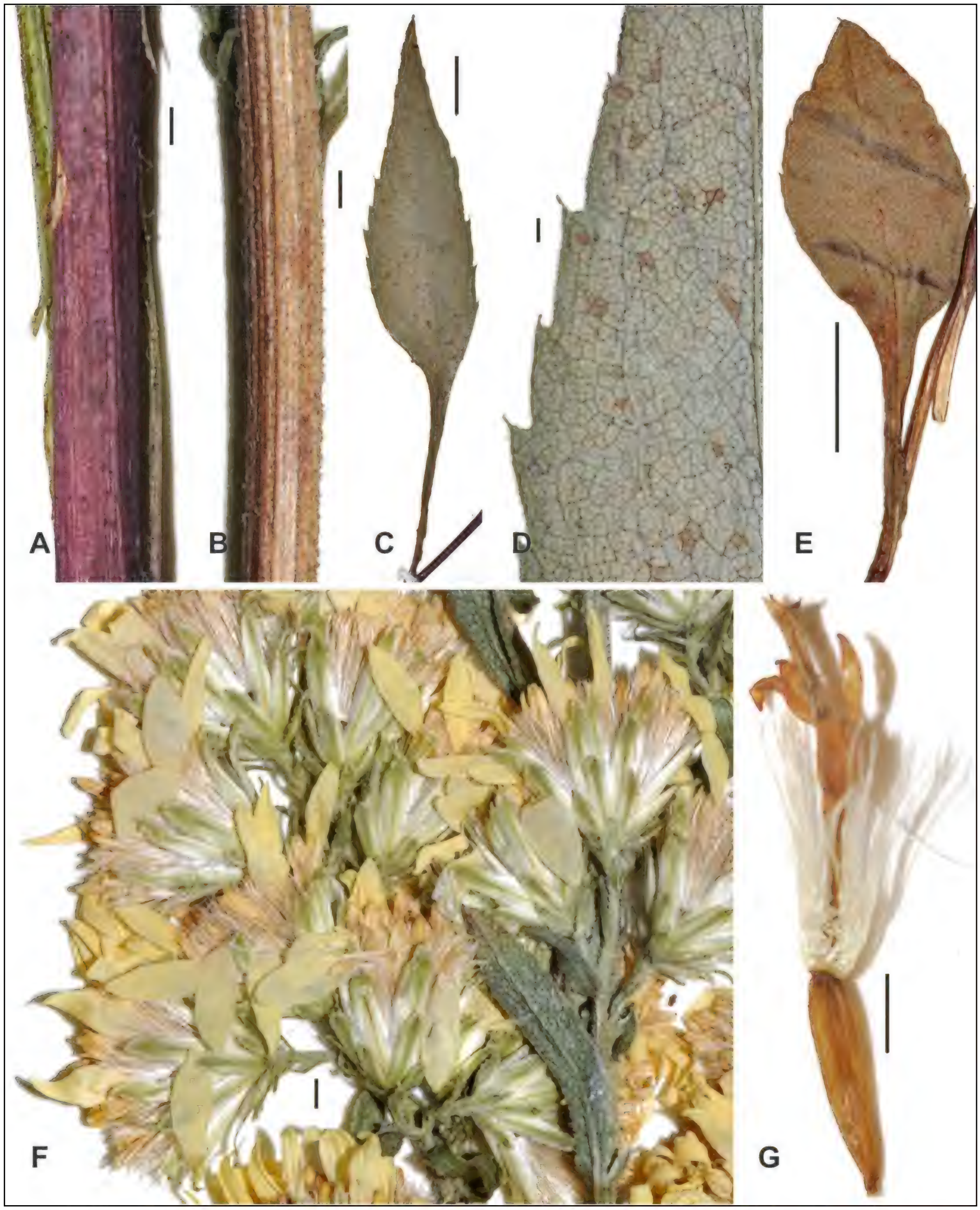

Figure 11. Details of the morphology of *Solidago decurrens*. **A-B.** Lower and upper stems, *Lin et al. 77* (A). **C-D.** Lower stem leaf and margin detail, *Lai & Shan 4428* (MO). **E.** Lower stem leaf, *Ding 526* (MO). **F.** Heads, *An 3963* (MO). **G.** Disc floret cypsela with corolla still attached, *Lin et al. 77* (A). Scale bars = 1 mm in A-B, D, and F-G = 1 cm in C and E.

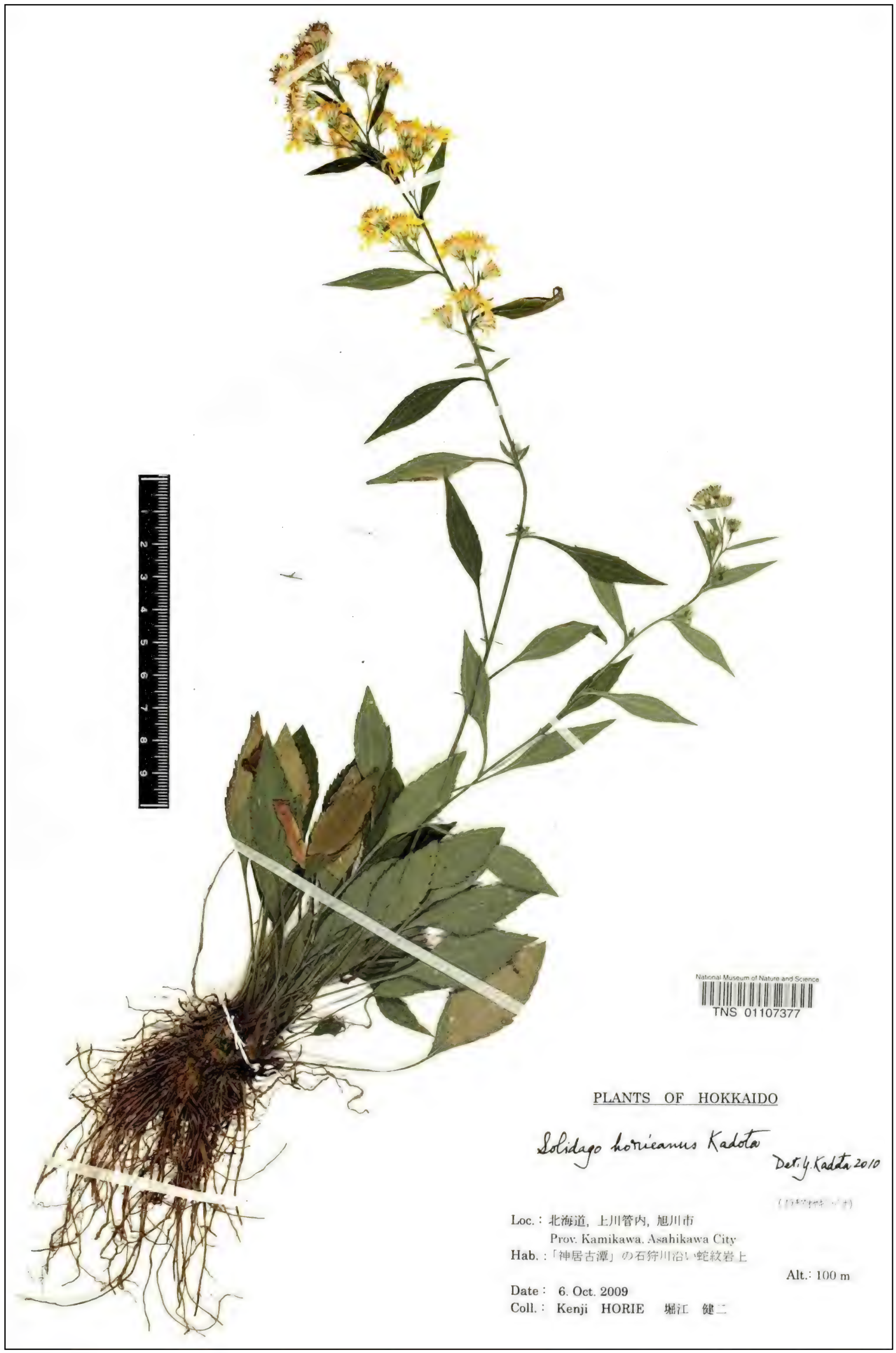

Figure 12. *Solidago horieana*, *Horie s.n.* (TNS) from Asahikawa, Hokkaido, Japan.

Figure 13. Large shoot of *Solidago kurilensis*, *Horii 1524* (KYO; holotype of *S. nipponica*).

Figure 14. Small shoots of *Solidago kurilensis*. **A.** *Yonekura 12919* (KYO), from Aomori Pref., Japan. **B.** *Barkalob s.n.* (ALA) from Iturup {Etorofu-to} Is., southern Kuril Islands, Kurilskyi Obl., Russia.

Figure 15. Details of the morphology of *Solidago kurilensis*. **A.** Lower stem and petiole base of lower stem leaf, *Barkalob s.n.* (ALA). **B.** Mid stem, *Hiroe 6808* (KYO). **C.** Small lower stem leaf, *Murata 6483* (KYO). **D.** Mid stem leaf, *Yonekura 12919* (KYO). **E.** Mid stem leaf margin, *Kurosaki 6416* (KYO). **F.** Heads, *Yonekura 12919* (KYO). **G.** Disc floret cypsela, *Kitamura s.n.* (KYO). Scale bars = 1 mm in A-B and F-G; = 1 cm in C- E.

Figure 16. Morphology of *Solidago minutissima* from Yakushima Is., Japan. **A.** Large shoot; *Furuse s.n.* (A). **B**. Small shoot; *Mitsuta 891* (KYO). **C.** Heads; *Murata 438* (KYO). **D.** Cypselae and old ray and disc corollas; *Mitsuta 891* (KYO). Scale bar = 1 cm in A and B; = 1 mm in C and D.

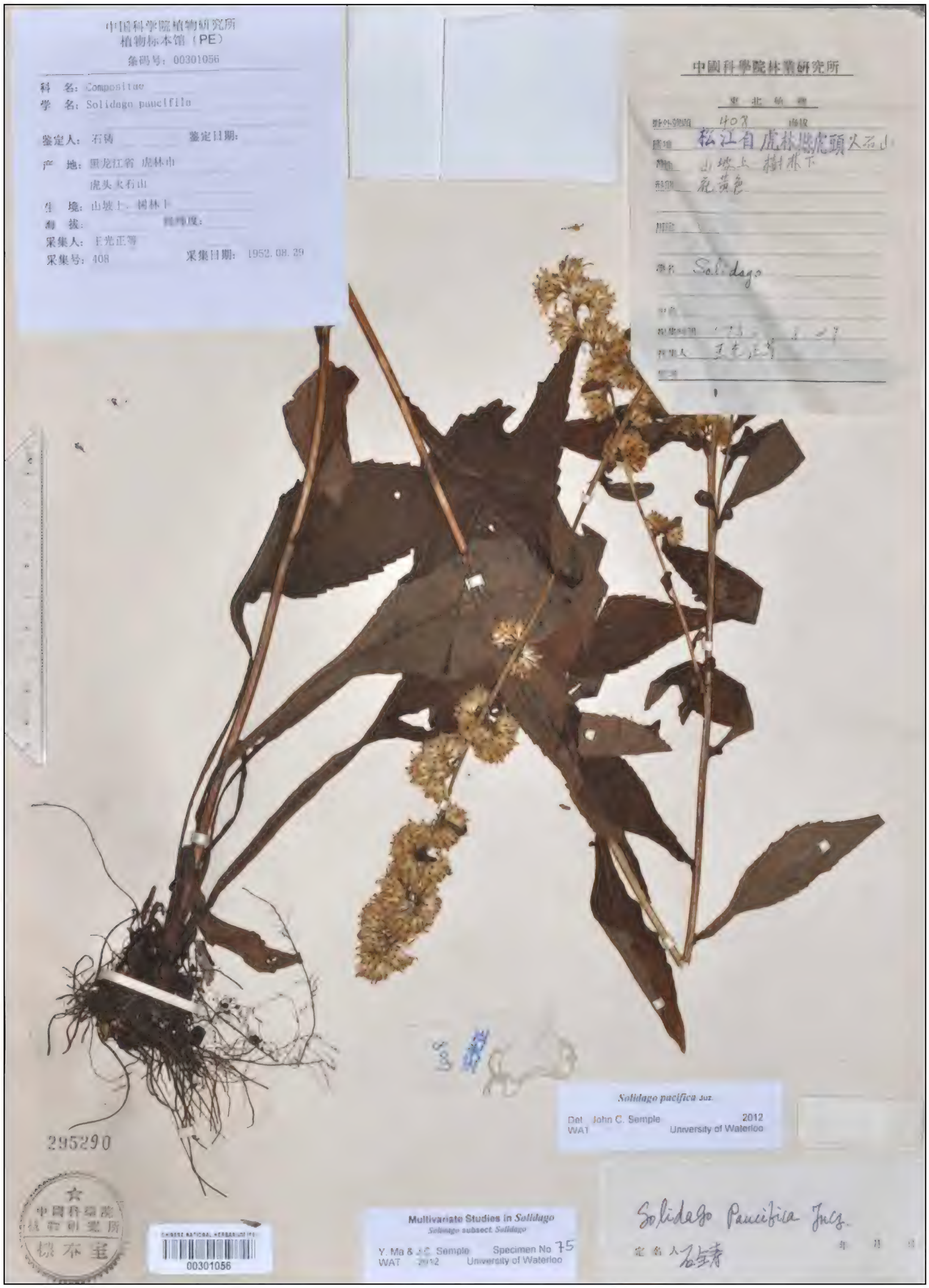

Figure 17. *Solidago pacifica*, *Wang et al. 408* (PE) from Heilongjiang Prov., China.

Figure 18. Details of morphology of *Solidago pacifica*. **A-B.** Lower and mid stems, *Wang et al. 408* (PE). C. Lower stem leaf, *Wang 563* (PE). **D.** Lower stem leaf venation, *Skvortsov s.n.* (MO). **E.** Stem leaf in inflorescence, *Wan & Chow 81116* (BM). **F.** Heads, *Wan & Chow 81116* (BM). **G.** Ray floret corolla and disc floret with immature cypsela, *Wang 592* (PE). **H.** Cypsela body, *Wan & Chow 81116* (BM). Scale bars = 1 mm in A-B and F-H-I = 1 cm in C-E.

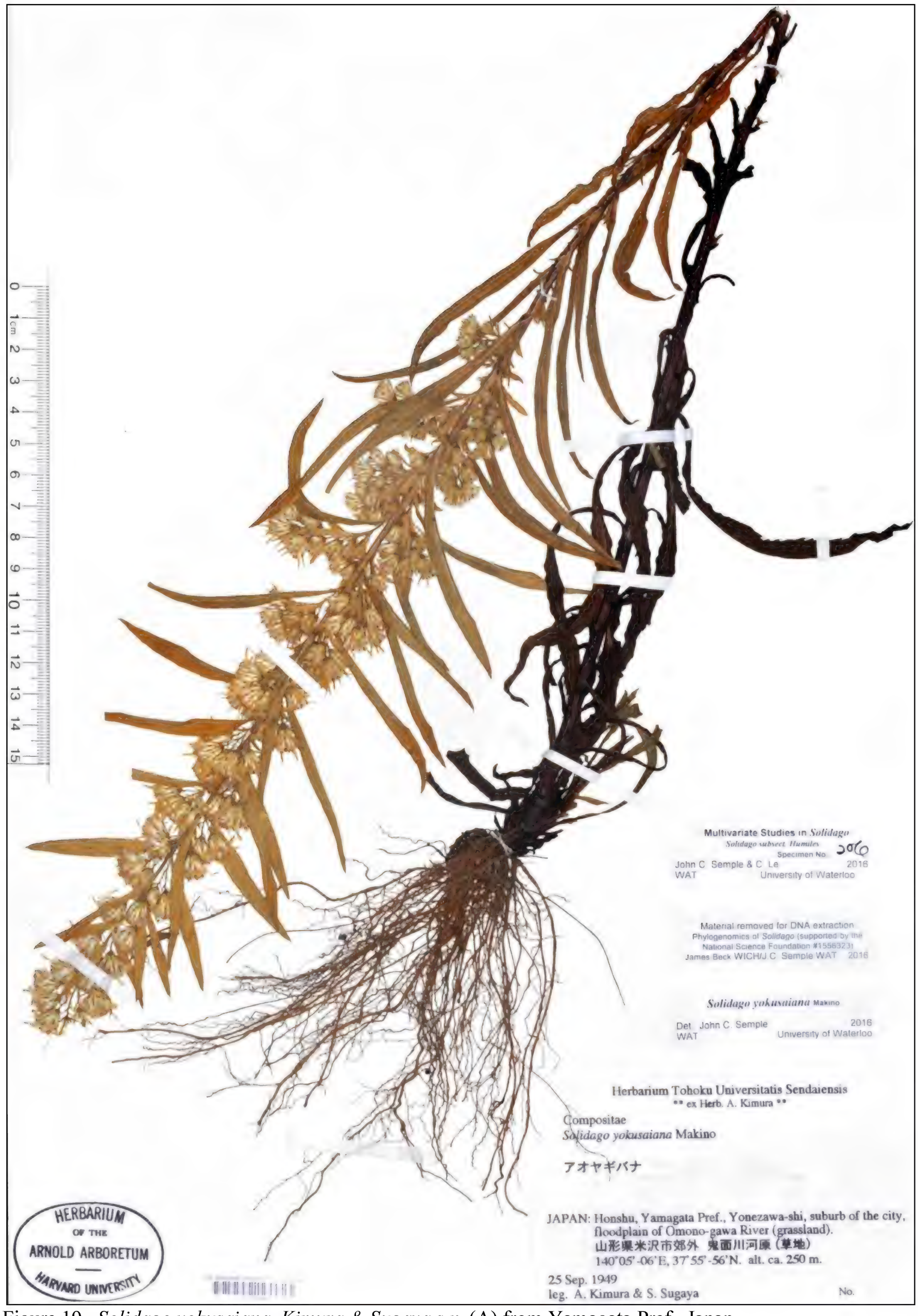

Figure 19. *Solidago yokusaiana, Kimura & Sugaya s.n.* (A) from Yamagata Pref., Japan.

Figure 20. Details of the morphology of *Solidago yokusaiana*. **A-B**. Lower and upper stems, *Furuse 1864* (K). **C.** Basal rosette leaves, *Furuse 1864 (*K). **D.** Lower stem leaf venation, *Tanaka {Beaudry} 58-320*-2 (MT). **E-F.** Mid and upper stem leaves, *Furuse 1864* (K). **G.** Heads, *Shiota 997* (GH). **H.** Disc floret with immature cypsela, *Lin et al. 77 (*A). **I.** Cypsela body, *Kimura & Sugaya s.n.* (A). Scale bars = 1 mm in A-B and G-I = 1 cm in C-F.

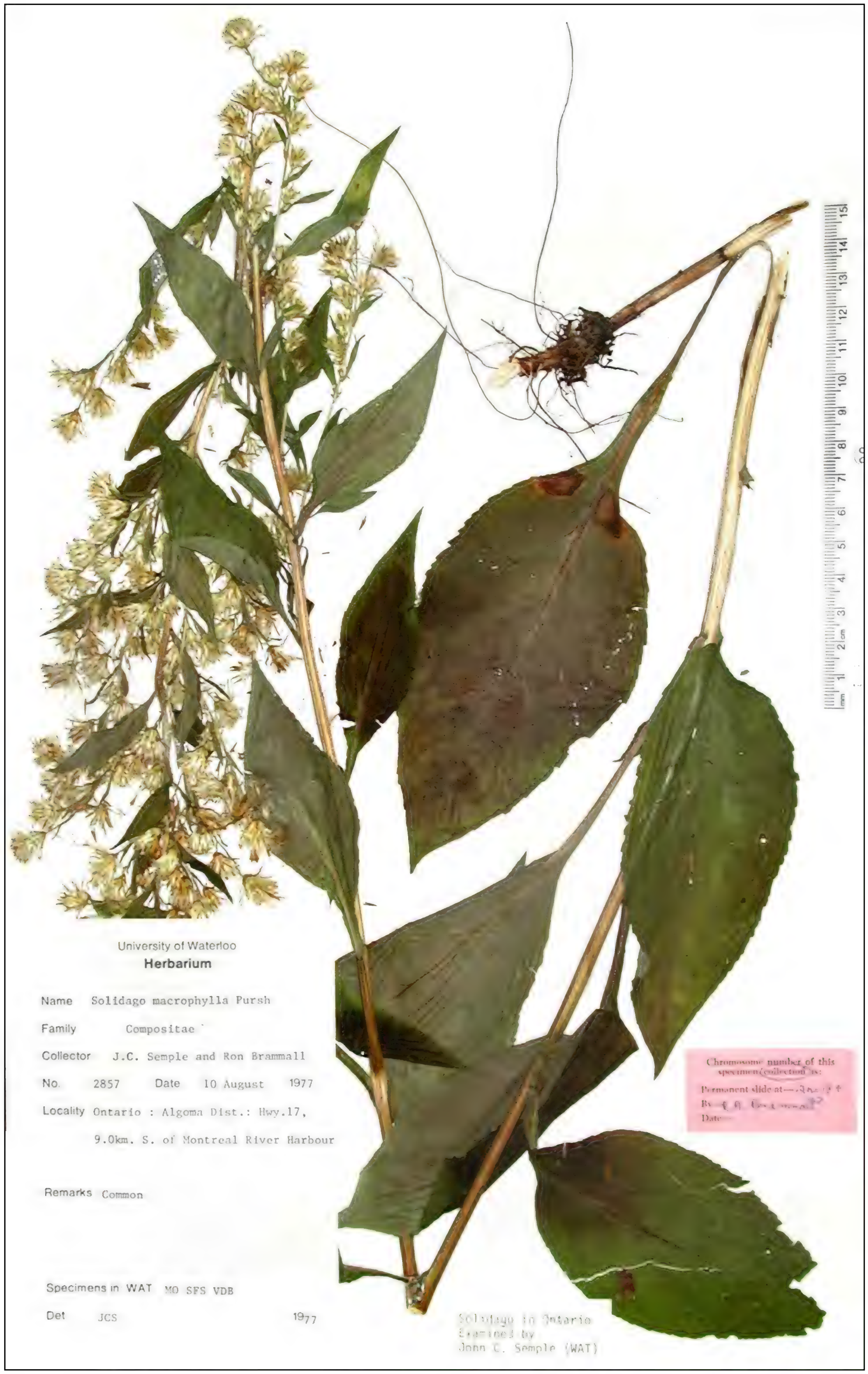

Figure 21. Large shoot of *Solidago macrophylla*, *Semple & Brammall 2857* (WAT) from Algoma Dist., Ontario.

Figure 22. Details of the morphology of *Solidago macrophylla*. **A**. Small shoot, *Legault et al. 8012* (MT). **B-C.** Lower and upper stems, *Morton & Venn NA12155* (WAT). **D.** Small lower stem leaf, *Dodson 25* (WAT). **E-F.** Lower mid stem leaf and undersurface midvein; *Rolland-Germain 776* (MT). **G.** Heads, *Dodson 25* (WAT). **H.** Disc floret cypsela with corolla still attached, *J. & B. Semple 6768* (WAT). Scale bars = 1 mm in B-C, and F-H; D-E = 1 cm in C and E; and A = 10 cm.

Figure 23. *Solidago multiradiata*, *Fraser 113 (WAT*) from northern Québec.

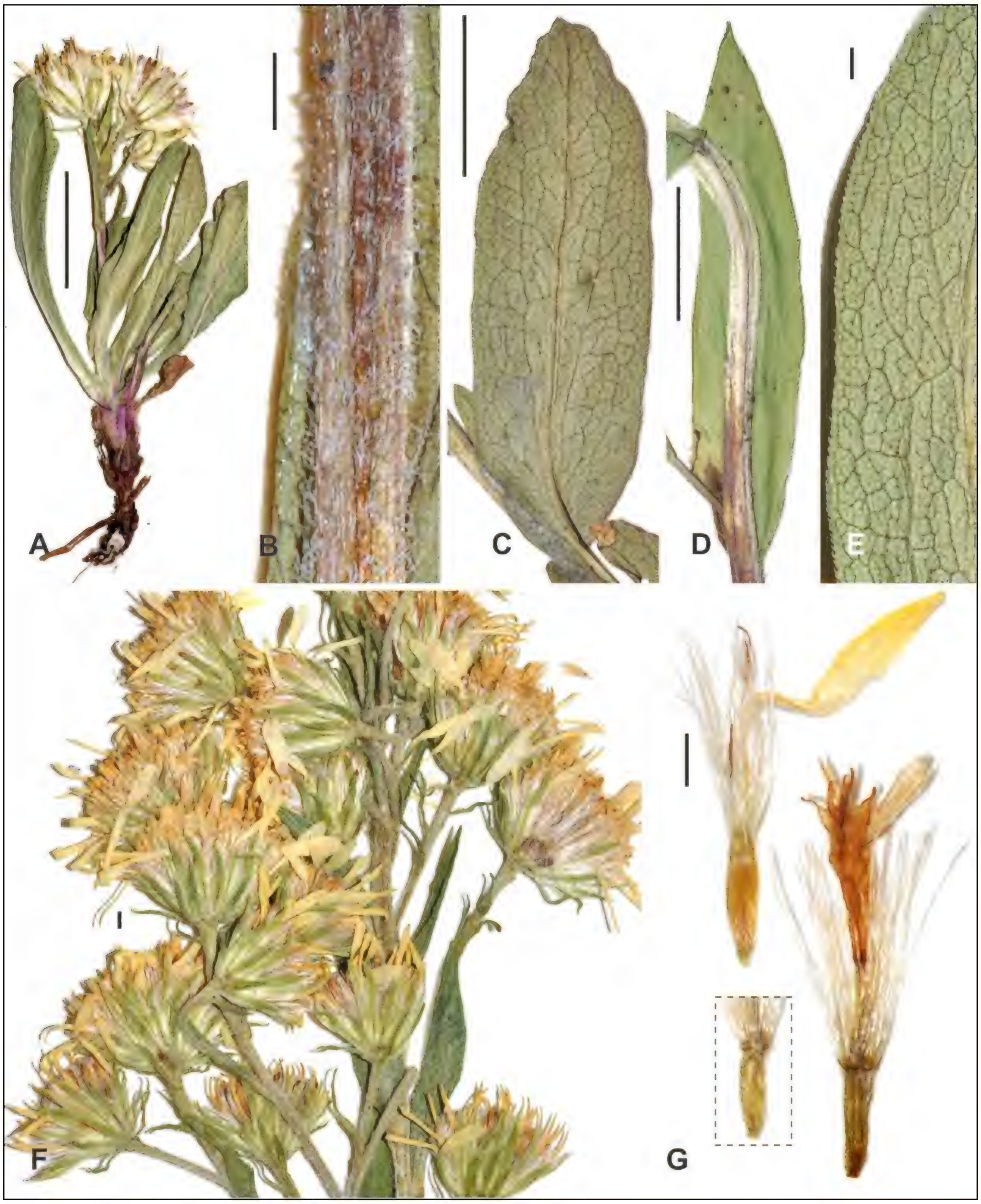

Figure 24. Details of the morphology of *Solidago multiradiata*. **A**. Dwarf shoot, *Semple et al 9227* (WAT). **B.** Upper stem, *van Varneveld JvB73-454* (V). **C-E.** Upper stem leaves and margin detail, *Hawthorn s.n.* (WAT), *Semple & Heard 8693* (WAT), and *Semple et al. 11165* (WAT).). **F.** Heads, *Clements s.n.* (WAT). **G.** Ray and disc floret cypselae with corollas still attached, *Semple et al. 11165* (WAT). Scale bars = 1 mm in B and F-G; = 1 cm in A and C-E.

Figure 25. *Solidago leiocarpa*, *Ringius 1617* (WAT) from Mt. Washington, New Hampshire.

Figure 26. Details of the morphology of *Solidago leiocarpa*. **A.** Upper stem, *Ringius 1588* (WAT). **B.** Basal rosette leaves, *Ringius 1566* (WAT). **C.** Mid stem leaves, *Ringius 1613* (WAT). **D-E.** Upper stem leaves in inflorescence, *Ringius 1617* (WAT) and *Ringius 1561* (WAT). **F.** Heads, *Ringius 1557* (WAT). **G.** Disc floret cypsela with corolla still attached, *Ringius 1617* (WAT). Scale bars = 1 mm in A and F-G; = 1 cm in B-E.

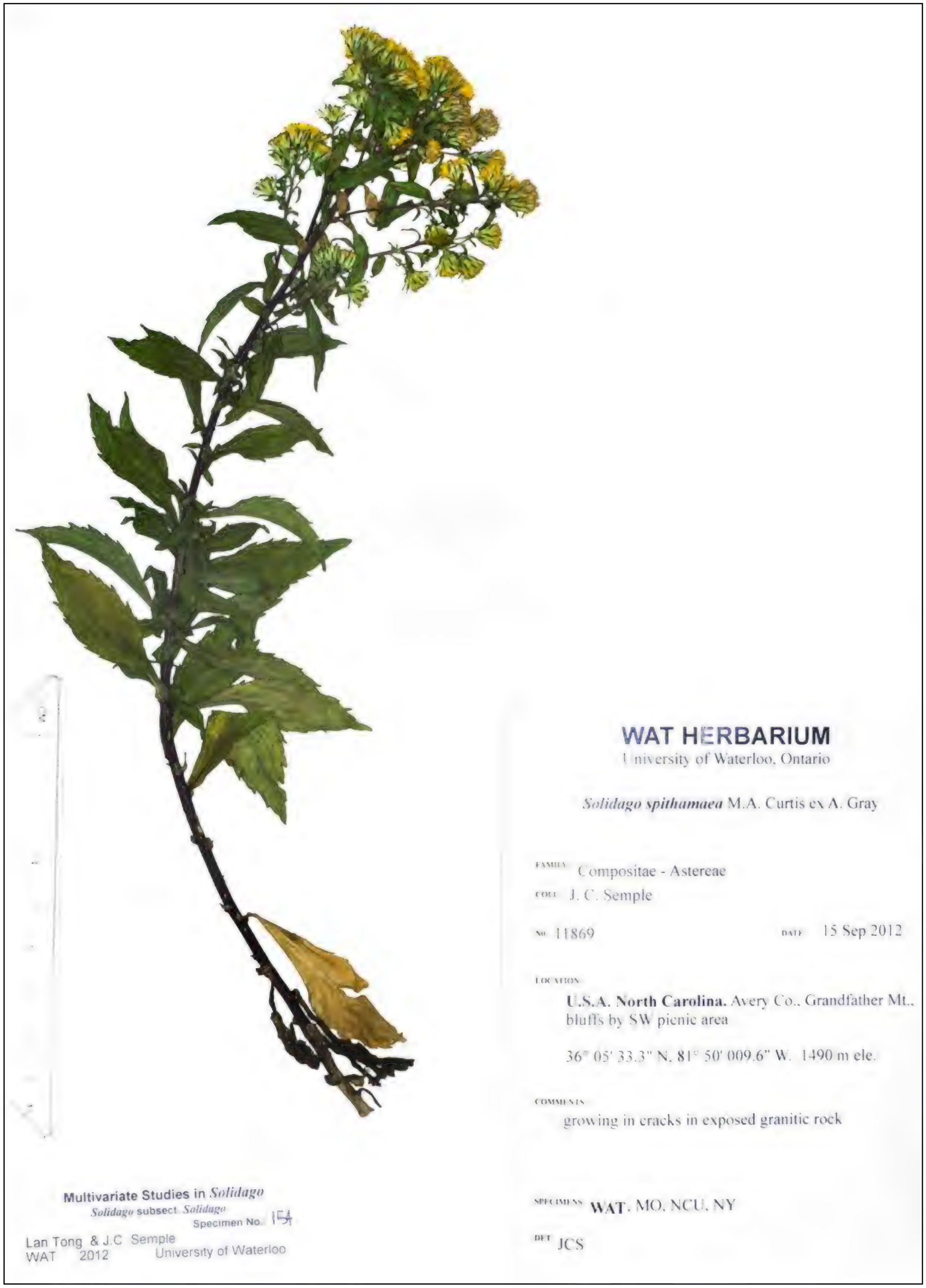

Figure 27. *Solidago spithamaea*, *Semple 11869* (WAT unmounted) from Avery Co., North Carolina.

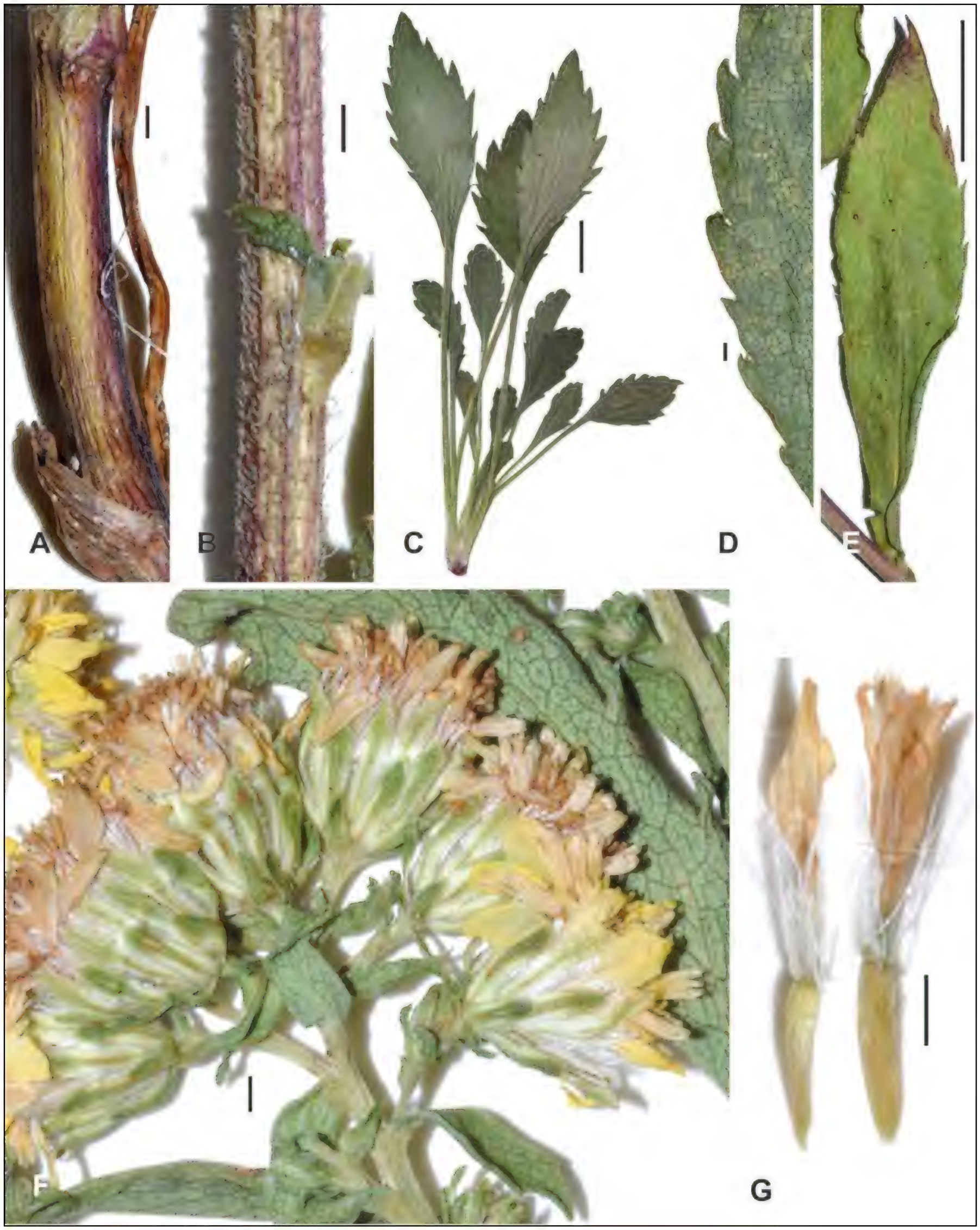

Figure 28. Details of the morphology of *Solidago spithamaea*. **A-B**. Lower and upper stems, *Semple & Suripto 9669* (WAT). **C.** Basal rosette leaves, *Semple 11869* (WAT). **D.** Lower stem leaf margin, *Semple & Suripto 9669* (WAT). **E.** Mid stem leaf, *Semple 11868* (WAT). **F.** Heads, *Semple 11869* (WAT). **G.** Ray and disc floret cypselae with corollas still attached, *Semple 11869* (WAT). Scale bars = 1 mm in A-B, D, and F-G; = 1 cm in C and E.

Table 1. Basionyms and combinations of species and infraspecific names of taxa proposed in the *Solidago virgaurea* complex occurring in far eastern Asia in chronological order of basionyms.

Solidago virgaurea L., Sp. Pl. 880. 1753. **SYNTYPES**: Europe. Herb. 998.15 (LINN!; **LECTOTYPE** designated by Garbari & Cecchi in C.E. Jarvis AND N. Turland (eds). 1998. Herb. Linn. 998.16 (LINN!). *Clifford 409*, Solidago 3 (BM). *Clifford 409*, Solidago 3a, (BM). *Clifford 409*, Solidago 3b, fol. A (BM). *Clifford 409*, Solidago 3b, fol. B (BM). *Clifford 409*, Solidago 3[e] (BM). Herb. Burser XV: 66 (UPS). Orthographic variant *S. virga-aurea*.

Solidago decurrens Loureiro, Fl. Cochinch. 501. 1790. **TYPE**: CHINA. Canton, date? Collector?. (HT: no collection seen at BM or P, F. Jabbour pers. com.). **NEOTYPE** (designated here: same as holotype of *Amphiraphis leiocarpa* Benth): CHINA. Hong Kong, 1841, *R.B. Hinds* (K!; Fig. 8).

Solidago cantoniensis Loureiro, Fl. Cochinch. 501. 1790. TYPE: CHINA. Canton, date? Collector? (HT: no collection seen at BM or P). **NEOTYPE** (designated here: same as holotype of *Amphiraphis leiocarpa* Benth): CHINA. Hong Kong, 1841, *R.B. Hinds* (K!; Fig. 8). = *S. decurrens* var. *decurrens*

Amphirhapis leiocarpa Benth. in Hook. f., Lond. J. Bot. 1: 488. 1842. *Solidago virgaurea* L. var. *leiocarpa* (Benth. in Hook.f.) A. Gray, Mem. Amer. Acad. n.s. 6(2): 395. 1859. non Miq. (1861). *Solidago virgaurea* L. var. *leiocarpa* (Benth. in Hook. f.) Nakai, Tokyo Bot. Mag. 31: 111. 1917. "in nota sub var. *coreana*", Nakai (1928). *Solidago virgaurea* L. subsp. *leiocarpa* (Benth. in Hook. f.) Hultén, Fl. Aleut. 315. 1937. **TYPE**: CHINA. Hong Kong, 1841, *R.B. Hinds* (T: K!; Fig. 8). = *S. decurrens* var. *decurrens*

Solidago virga-aurea L. var. *leiocarpa* Miquel, Neerl. J. Bot. 1: 101. 1861. non (Benth in Hook.f) Nakai (1917). **TYPE**: CHINA. Croit sur la montagne de Samkok, Su-heang, Oct, *??* (Type: not seen) No type specimens in L or U at Leiden, Netherlands (email from collections manager Thiejsse, 3 Apr 2013). = *S. decurrens* var. *decurrens*

Solidago virgaurea var. *taquetii* Lével. & Vaniot, Fedde Rep. 8: 141. 1910. **TYPE**: South Korea. Quelpaert, in herbidis Hioton, 22 Aug 1908, *Taquet 940* (holotype: E digital image e00413380! jstor.org) = *S. decurrens* var. *decurrens*

Solidago yokusaiana Makino, Tokyo Bot. Mag. 28: 179. 1914. nom. nov. for *Solidago virgaurea* var. *angustifolia* Makino (1898). "Japan, southern. This grows always on rocks by rivers" **TYPE**: JAPAN. River side of Niyodo River, Ochi Village,Takaoka Country, Tosa, 30 Oct. 1891, *K. Watanabe s.n.* (lectotype designated by Semple & Ohi-Toma 2017: TI digital image from TI!).

Solidago virgaurea L. var. *minutissima* Makimo, Tokyo Bot. Mag. 28: 179. 1914. *Solidago minutissima* (Makino) Kitamura, Acta Phytotax. Geobot. 3: 141. 1934. **TYPE**: JAPAN. {Kagoshima Pref., Kumage Co., Kamiyaku Town, Miyanoura} Prov. Osumi, Mt. Miyanoura-dake in Isl. Yakusima, Sep 1909, *T. Makino s.n.* (lectotype designated by T. Yahara, J. Fac. Sci. Univ. Tokyo 1987: MAK-175611 digital image on line!, digital image sent by MAK!).

Solidago virgaurea L. var. *coreana* Nakai, Bot. Mag. (Tokyo) 31(364): 110 (-111). 1917. Sylv. Koreana 14: 122. 1922. *Solidago decurrens* var. *coreana* (Nakai) Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 397. 1937. **TYPE**: Korea. in monte Bi-ru-bon, 16 Aug 1916, *Nakai 5921* (holotype: TI, digital image TI00011104 sent by Tetsuo Ohi-Toma from TI!).) = *S. decurrens* var. *decurrens*

Solidago virgaurea var. *asiatica* Nakai, Tokyo Bot. Mag. 42: 16. 1928. nom. invalid., nom. nud. "common in East Asia".) = *S. decurrens* var. *decurrens*

Solidago virga-aurea L. var. *yakusimensis* Nakai, Tokyo Bot. Mag. 62: 16. 1928. *Solidago yakusimensis* (Nakai) Masam., Mem. Fac. Sc. & Agric. Taihoku Imp. Univ. xi., Bot. No. 4, 439. 1934. **TYPE**: JAPAN. Kyushu Is. Prov. Osumi, in montibus insl.Yakusima, s.d., *Y. Yoshii* s.n. (holotype: TI, digital image TI00011108! sent by Tetsuo Ohi-Toma). = *S. minutissima*

Solidago virgaurea var. praeflorens Nakai, Tokyo Bot. Mag. 42: 16. 1928. *Solidago decurrens* Loureiro var. *praeflorens* (Nakai) Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 397. 1937. **TYPE**: JAPAN. Hachijyo Is., 15 Jun 1920, *J. Nakai s.n.* (holotype: TI, digital image TI0001110x sent by Tetsuo Ohi-Toma from TI! Fig. 10). = *Solidago decurrens* var. *praeflorens*

Solidago hachijoensis Nakai, Tokyo Bot. Mag. 42: 16. 1928. nom. nud. validly published in Tokyo Bot. Mag. 42: 472. = *S. decurrens* var. *praeflorens*

Solidago virga-aurea L. var. *gigantea* Nakai, Tokyo Bot. Mag. 62: 17. 1928. **TYPE**: JAPAN. {Hokkaido: Hokkaido Pref.,} Yeso, Nayoro Prov., {Teshio Dist.}, Teshio, 30 Aug 1919, *Nakai s.n.* (holotype: TI Herb. Imp. Univ., 3 sheets, one shoot in three parts) digital image provided by herbarium!) = *S. pacifica*

Solidago japonica Kitamura, Acta Phytotax. Geobot. 1932, 1(4): 286, in obs. **TYPE**: JAPAN. Hondo. Prov. Yamashiro, Mt. Hiei, Oct 1920, *G. Koidzum*i (Holotype: KYO, not seen). = *S. decurrens* var. *decurrens*

Solidago mirabilis Kitamura, Acta Phytotax. Geobot. 3: 140. 1934. non Small (1933). **TYPE**: JAPAN. Hondo. Prov. Ugo, Peninsula Oga, Shiodo, 4 Oct 1931, *H. Muramatsu s.n.* (holotype: not seen). = *S. kurilensis*

Solidago insularis Kitamura, Acta Phytotax. Geobot. 3: 141. 1934. *Solidago virgaurea* L. var. *insularis* (Kitam.) Hara, Enum. Spermatophytarum Japon. 2: 261 (1952). ***Solidago decurrens*** Loureiro var. ***insularis*** (Kitamura) Semple, comb. nov. **TYPE**: JAPAN. Liukiu, Is. Amani-oshima, Kaneku, 24 Apr 1923, *G. Kordsumi* (holotype: KYO, digital image!; Fig. 9) -Typus, Koniya, Dec. 1916 *leg?* (KYO, not seen), Insul. Utchina, Nawa, 3 Jan 1924, *Z. Tashiro* (KYO, not seen), Nakagamigun, Minjatomura, Osato, 9 Apr 1934, *N. Tawada* (KYO, not seen). = *S. decurrens* var. *insularis*

Solidago virgaurea L. var. *dahurica* Kitagawa, Rep. Inst. Sci. Res. Manchouchuo 1: 297(-298; t. 3, fig. 2). 1937. *Solidago dahurica* Kitagawa, Rep. Inst. Sci. Res. Manchoukuo 1: 297, in syn., as Kitag. mss. 1937. *Solidago virgaurea* L. subsp. *dahurica* (Kitag.) Kitag., Rep. Inst. Sci. Res. Manchoukuo 3(App. 1): 472. 1939 [Oct 1939]. *Solidago dahurica* (Kitag.) Kitag. ex Juz., Fl. URSS 25: 42. 1959. **TYPE**: CHINA. Heilongjiang Prov., "Prov. Hsing-an Orient, near Buheto", 22 Aug 1936, *Kitagawa s.n.* (Holotype: photograph in protologue!, digital image TI00011101 sent by Tetsuo Ohi-Toma from TI!).

Solidago virgaurea var. *paludosa* Honda, Bot. Mag. Tokyo 40: 95. 1937. *Solidago japonica* var. *paludosa* (Honda) Honda, Bot. Mag. Tokyo 40: 645. 1937. *Solidago decurrens* f. *paludosa* (Honda) Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 396. 1937. **TYPE**: JAPAN. Honshu. Prov. Sinano, n monte Kirigamine, 28 Jul1936, *T. Osaka 34* (holotype: TI digital image TI00011103! sent by Tetsuo Ohi-Toma) = *S. decurrens* var. *decurrens*

Solidago hachijoensis var. *elata* Honda, Tokyo Bot. Mag. 51: 645. 1937. **TYPE**: JAPAN. Honshu. Osima, Prov. Izu, 1936, *J. Iwata* (H: Herb. Imp. U. Tokyo, not seen).

Solidago virgaurea subsp. *asiatica* Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 398. 1937. nom. nud. in syn.

Solidago virgaurea var. *asiatica* Nakai ex Hara, Bot. Mag. 52: 128. 1938 [nom. & stat.nov.], replaced syn. *Solidago japonica* Kitamura (1932). *Solidago virgaurea* subsp. *asiatica* (Nakai ex Hara) Kitam. ex Hara, Enum. Sperm. Jap. 2: 260. 1952. **TYPE**: same as *S. japonica* Kitamura. JAPAN. Hondo. Prov. Yamashiro, Mt. Hiei, Oct 1920, *G. Koidzumi* (holotype: KYO, not seen). = *S. decurrens* var. *decurrens*

Solidago pacifica Juz., Fl. URSS xxv. 576. 1959. **TYPE**: RUSSIA. Distr. Vladivostok, reg. Suifunensis, in vicin. Nikolsk-Ussuriensis, Krasnojarskayi sopka (ad fl. Suifun), 5 Sep 1927, *W. Transzchel sub n° 534* (holotype: LE digital image LE-01012705! provided by LE Aug 2015).

Solidago kurilensis Juzepczuk in Komarov, Fl. URSS, xxv. 577. 1959. *Solidago virgaurea* L. subsp. *kurilensis* (Juz.) V.N.Voroschilov in A.K. Skvortsov (ed.), Florist. issl. v razn. raionakh SSSR: 193 (1985): 1985. **TYPE**: RUSSIA. Insulae Kurilensis Merdionales, ins. Sikotan, in declivibus montium et in pratulis insularum Kurilensium, 27 Aug 1948, *A.I. Gizenko* (holotype: LE digital image LE-01012704 provided by LE Aug 2015).

Solidago horieana Kadota, J. Jap. Bot. 83(4): 235 (233-238; figs. 1-3, map). 2008 [Aug 2008]. **TYPE**: JAPAN. Hokkaido Island: Sorachi Subpref., Uryu-gun, Horokanai-cho, Osarunai, along the valley of Osarunai-gawa, 44° N, 142° 6' 34" E, 140 m, 7 Jul 1991, *K. Horie s.n.* (holotype: TNS 769414, digital image sent by Shinobu Akiyama Mar 2017; isotypes: KYO, SAPT, TI, TNS 769410, digital image sent by Shinobu Akiyama! Mar 2017, TNS 769411 digital image! sent by Shinobu Akiyama Mar 2017, TNS 769412, digital image! sent by Shinobu Akiyama Mar 2017, TNS 769413, digital image! sent by Shinobu Akiyama Mar 2017).

Solidago nipponica Semple, Phytoneuron 2013-24: 1–9. 2013. **TYPE**: JAPAN. Honshu: Akita Pref., Oga city, Motoyama, 140 m ele., 21 Sep 1997, *Yojiro Horii 1524* (KYO!) = *S. kurilensis*

The purpose of this study was to determine statistical support for recognizing the species and varieties proposed within *Solidago* sect. *Solidago*, the levels of distinctiveness among the taxa, and what technical traits can be used to separate taxa besides those used to define the taxa as groups a priori. Also, taxa in ser. *Solidago* are compared with *S. macrophylla* and the three species of sect. *Multiradiatae*. The latter two North American taxa have been considered to be closely related to *S.* ser. *Solidago*. This is viewed as a preliminary study because not all taxa are included or available samples sizes were too small to include a taxon as an a priori group. No previous multivariate study has included all these species.

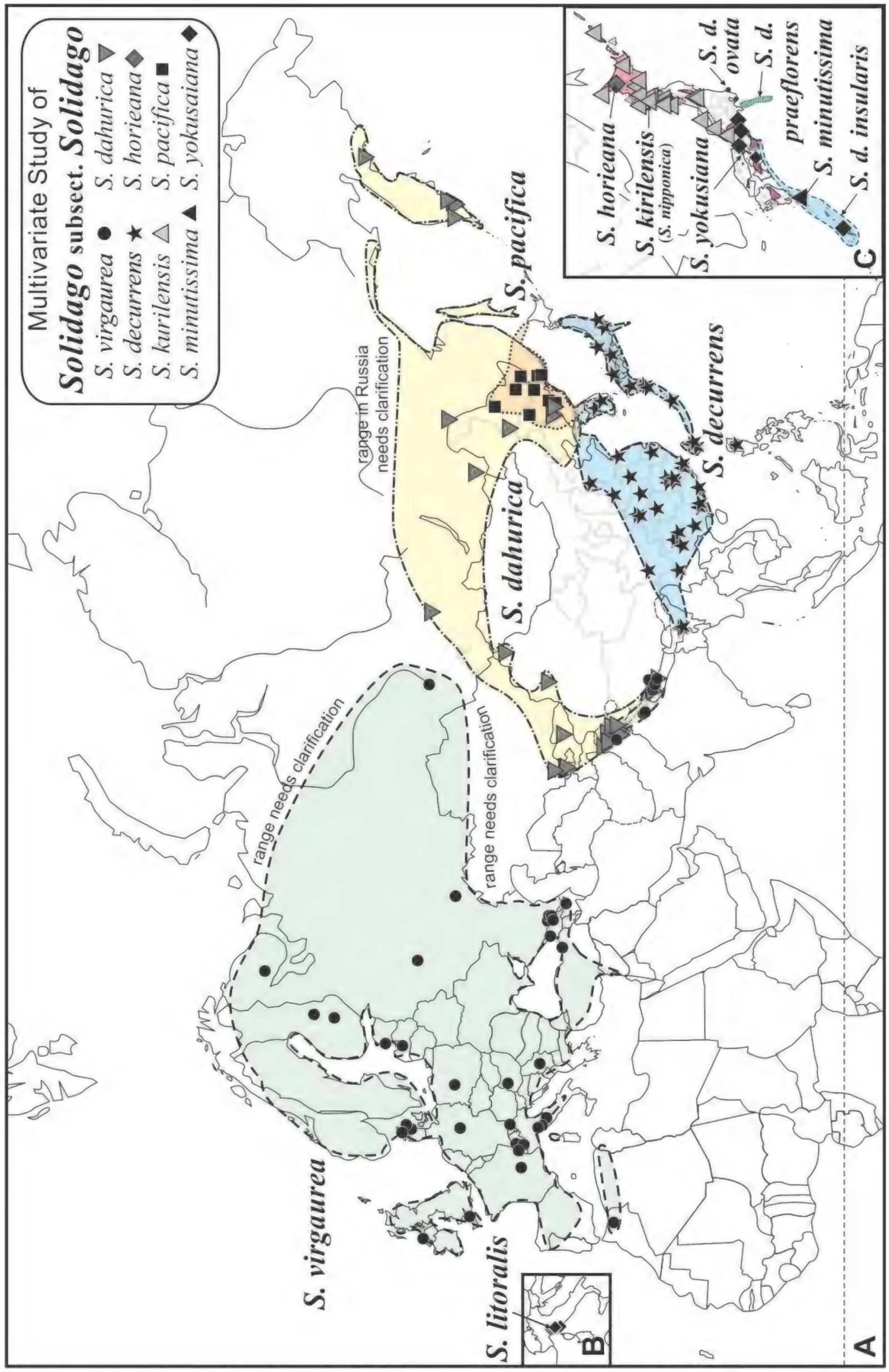

Figure 29. Ranges of distribution of taxa in *Solidago* ser. *Solidago* based on all collections seen and literature and locations of samples included in the multivariate analyses. **A.** Eurasia. **B.** Italy. **C.** Japan.

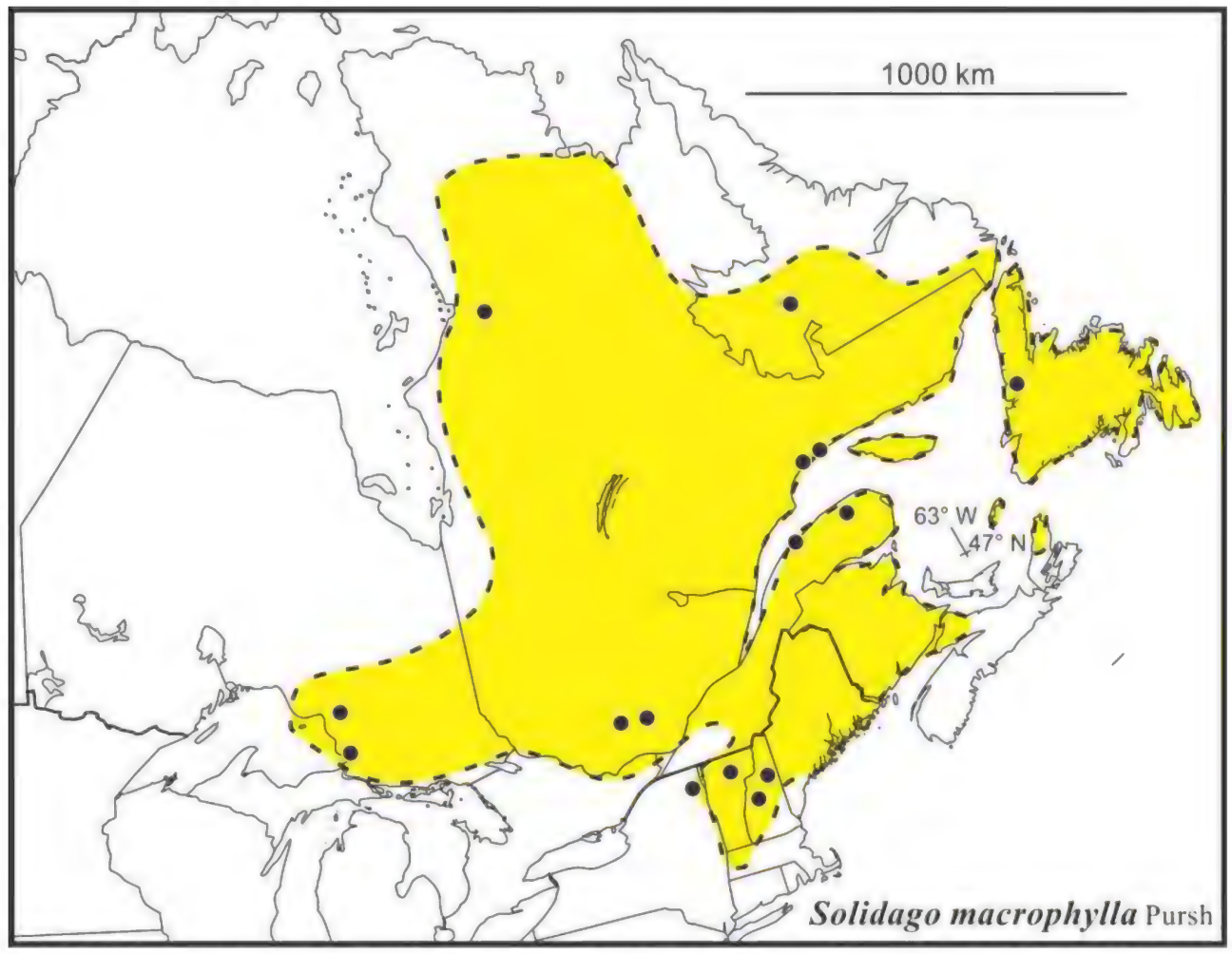

Figure 30. Range of distribution of *Solidago macrophylla* in eastern Canada and the adjacent US based on all collections seen and literature and locations of samples included in the multivariate analyses.

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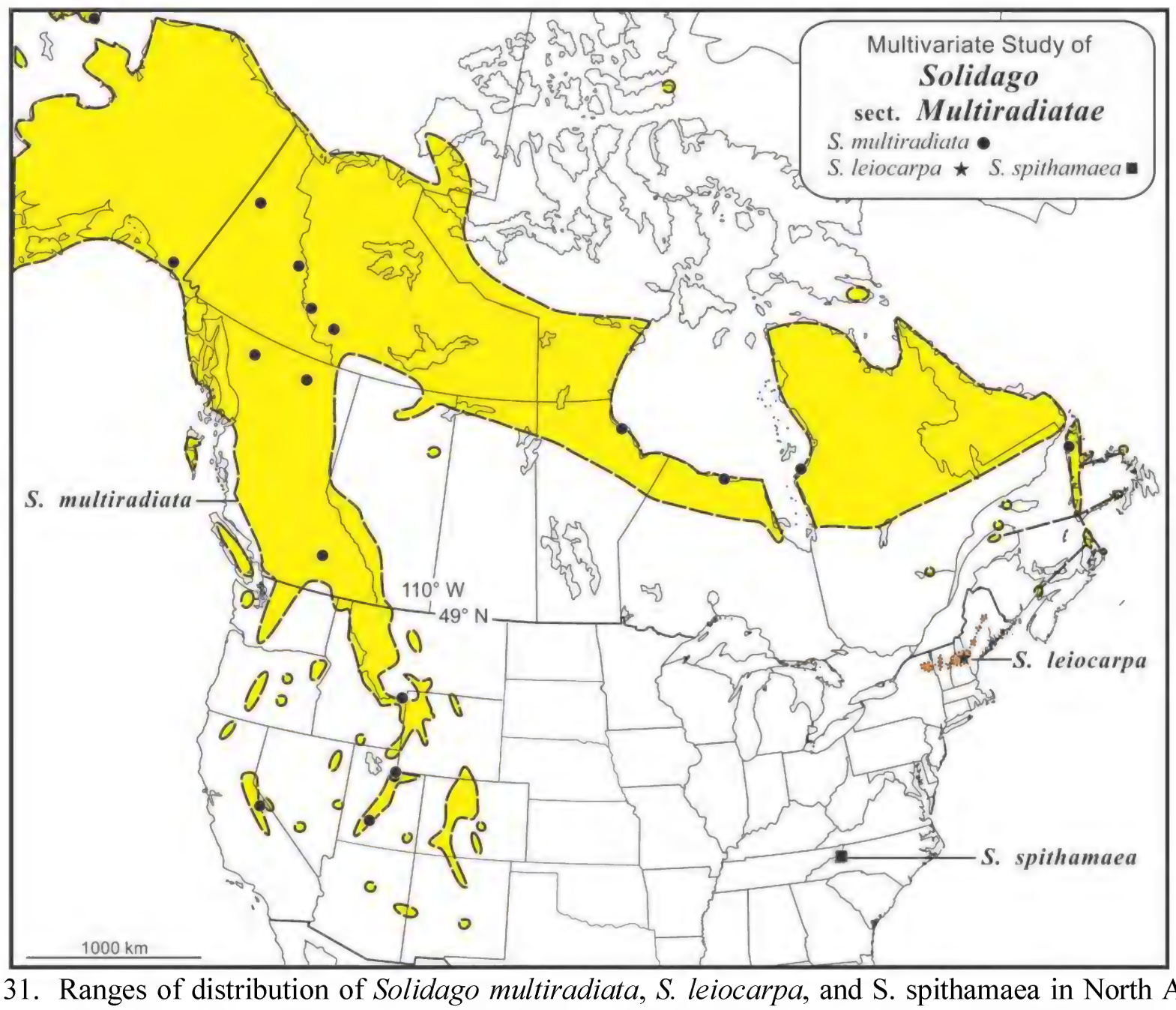

Figure 31. Ranges of distribution of *Solidago multiradiata*, *S. leiocarpa*, and S. spithamaea in North America based on all collections seen and literature and locations of samples included in the multivariate analyses.

MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria: A, ALA, BM, GH, the J.K. Morton personal herbarium in TRT, K, KYO, MO, MT, PE, PI, TNS, WAT in MT (Thiers continuously updated). More than 1100 specimens were examined, from which 217 were chosen and measured for the statistical analyses based on completeness of the specimen, maturity, and geographical distribution: 161 specimens of ser. *Solidago* (36 specimens of *Solidago virgaurea* s.s., 25 specimens of *S. dahurica*, 44 specimens of *S. decurrens* including 5 specimens of var. *insularis*, 1 specimen of *S. horieana*, 20 specimens of *S. kurilensis* including the holotype of *S. nipponica*, 8 specimens of *S. litoralis*, 13 specimens of S. *minutissima*, 9 specimens of *S. pacifica*, and 5 specimens of *S. yokusaiana*) and 56 specimens of possibly related North American species (13 specimens of *S. leiocarpa*, 13 specimens of *S. macrophylla,* 17 specimens of *S. multiradiata* and 13 specimens of *S. spithamaea*). In total, 18 vegetative and 16 inflorescence and floral traits were scored for the final analyses (Table 2). Additional stem, leaf, inflorescence, and phyllary and cypsela indument traits were used in assigning specimens to a priori groups.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016) and are not repeated here. Seven analyses were performed. In the first analysis, *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. litoralis*, *S. macrophylla, S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea*, and *S. virgaurea* were included in a STEPWISE discriminant analysis and then a COMPLETE discriminant analysis with seven traits because only eight specimens of *S. litoralis* were included. In the second analysis, three a priori groups (ser. *Macrophyllae*, sect. *Multiradiatae*, and ser. *Solidago*) were included in a STEPWISE discriminant analysis. In the third analysis, *S. leiocarpa*, *S. multiradiata*, and *S. spithamaea* were included in a STEPWISE discriminant analysis. In the fourth analysis, *S. dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea*, were included in a STEPWISE discriminant analysis. In the fifth analysis, *S. litoralis* and *S. virgaurea* were compared in a STEPWISE discriminant analysis. In the sixth, *S. dahurica*, *S. decurrens*, and *S. virgaurea* were investigated via a STEPWISE analysis. In the seventh, *S. decurrens*, *S. kurilensis*, and *S. minutissima* were included in a STEPWISE discriminant analysis with specimens of *S. decurrens* var. *insularis*, *S. horieana*, and *S. yokusaiana* included a posteriori. Numerous preliminary analyses were run over multiple years as the sample sizes of the taxa were increased but are not reported here. One result of these preliminary analyses was the conclusion that *S. nipponica* was a synonym of *S. kurilensis*.

Table 2. Traits scored for the multivariate analyses of 217 specimens of *Solidago*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)

MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of the inflorescences at the widest point (cm).
CAPBLN	Length of the lower longest inflorescence branches (cm)
INVOLHT	Involucre height at anthesis (mm)
MIDPHYLWD	Width of mid series phyllary at widest point (mm)
MIDPHYLW1MM	Width of mid series phyllary 1 mm below apex (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DACHPUB	Total number of hairs on disc floret ovary/fruit body

RESULTS

Eleven species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to the length of the mid stem leaf and the number of mid stem leaf margin serrations. Basal rosette leaves were often not present and were not included in the analyses. Lower stem leaves were present on many specimens but were not included in the analyses because their traits correlated highly among themselves and with mid and upper stem leaf traits. Among the floral traits scored the following pairs of traits correlated highly: ray floret lamina length and disc floret pappus length, ray floret ovary/fruit body length and disc floret ovary/fruit body length, ray floret pappus length and disc floret pappus length, and disc corolla length and disc floret pappus length correlated highly; the underlined characters were included in the analyses.

In the COMPLETE discriminant analysis of 206 specimens of eleven species level a priori groups (*Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea,* and *S. virgaurea*), the following seven of twelve traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: total number of disc floret ovary/fruit body hairs (33.63), mid series phyllary length (17.28), number of mid stem leaf margin serrations (16.96), number of ray florets (14.75), mid stem leaf length (11.96), mid series phyllary width 1 mm below apex (10.37), disc corolla lobe length (4.02). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 3. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. macrophylla* and *S. multiradiata* (58.318); the smallest separations were between *S. litoralis* and *S. spithamae* (4.559).

Table 3. Between groups F-matrix for the 11 a priori group analysis (df = 7 189).

Group	*dahurica*	*decurrens*	*kurilensis*	*leiocarpa*	*litoralis*	*macrophylla*	*minutissima*	*multiradiata*
decurrens	13.146							
kurilensis	15.060	19.816						
leiocarpa	25.682	36.000	29.797					
litoralis	14.301	19.603	18.891	1.226				
macrophylla	22.328	52.913	42.310	37.800	28.200			
minutissima	23.961	10.524	15.270	38.526	23.261	50.959		
multiradiata	34.185	41.676	31.314	23.448	16.850	58.318	31.927	
pacifica	4.922	4.532	11.358	17.403	12.157	24.464	14.928	26.154
spithamaea	15.408	19.203	13.310	7.438	4.559	27.839	20.826	25.142
virgaurea	15.334	22.882	9.414	15.994	6.470	52.969	23.681	23.729

Group	*pacifica*	*spithamaea*
spithamaea	12.714	
virgaurea	11.370	9.452

Wilks' lambda = 0.0086 df = 7 10 195; Approx. F= 19.9746 df = 70 1108 prob = 0.0000

In the Classificatory Discriminant Analysis of 206 specimens of the 11 species level a priori groups (*Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. litoralis*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea,* and *S. virgaurea*), percents of correct a posterori assignment to the same a priori group ranged from 56-100%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results are presented in order of decreasing percents of correct placement. Thirteen of 13 specimens of the *S. minutissima* a priori group (100%) were assigned a posteriori to the *S. minutissima* group with 93-100% probability. Twelve of 12 specimens of the *S. macrophylla* group (100%) were assigned a posteriori to the *S. macrophylla* group with 99-100% probability. Fifteen of the 17 specimens of the *S. multiradiata* a priori group (88%) were assigned a posteriori to *S. multiradiata* groups (88%): 13 specimens with 99-100% probability and 2 specimens with 87% and 82% probabilities. One specimen of the *S. multiradiata* a priori group a priori group (85%) was assigned a posteriori to *S. virgaurea* with 49% probability (23% to *S. dahurica*, 13% to *S. decurrens* and 9% to *S. multiradiata* (*Semple et al. 11165* WAT from Nahanni N.P.R., Northwest Terr., Canada). Eleven of 13 specimens of the *S. spithamaea* a priori group were assigned a posteriori to the *S. spithamaea* group: 5 specimens with 94-99% probability, 1 specimen with 65% probability, 1 specimen with 56% probability, and 4 specimens with 45-49% probability (all 11 from Grandfather Mt., North Carolina). Two specimens of the *S. spithamaea* a priori group were assigned a posteriori to other species: 1 specimen to *S. dahurica* with 49% probability (26% to *S. spithamaea* and 22% to *S. macrophylla* (*Semple & Suripto 9669* WAT) and 1 specimen to *S. kurilensis* with 41% probability (32% to *S. spithamaea* and 22% to *S. virgaurea*; *Semple & Suripto 9669* WAT). Sixteen of 20 specimens of the *S. kurilensis* a priori group (85%) were assigned a posteriori to the *S. kurilensis* group: 7 specimens with 92-100% probability (including a shoot of *Barkalob s.n.* ALA from the southern Kuril Islands), 3 specimens with 83-89% probability, 2 specimens

with 77% and 73% probabilities, 1 specimen with 68% probability (the holotype of *S. nipponica*, *Horii 1524* KYO; Fig. 13), 1 specimen with 57% probability (22% to *S. virgaurea*), and 2 specimens with 42% probability (42% to *S. spithamaea* and 16% to *S. virgaurea*) and 42% probability (30% to *S. minutissima* and 22% to *S. decurrens*). Three specimens of the *S. kurilensis* a priori group were assigned to other species: 1 specimen to *S. virgaurea* with 92% probability (*Konta 19657* A from Aomori Pref., Japan) and 2 specimens to *S. decurrens* with 60% probability (17% to *S. kurilensis* and 9% to *S. dahurica*; *Staff of Bot. Gard. Tohoku U. 72905* MO from Ogachi-gun, Akita Pref., Japan) and 54% probability (28% to *S. minutissima* and 7% to *S. kurilensis*; *Kurosaki 6416* KYO from Hokkaido, Japan). Thirty-seven of 44 specimens of the *S. decurrens* a priori group (84%) were assigned a posteriori to the *S. decurrens* group: 3 specimens with 90-93% probability, 12 specimens with 81-89% probability, 8 specimens with 73-79% probability, 6 specimens with 60-68% probability, 6 specimens with 50-58% probability, and 2 specimens with 46% probability (23% to *S. pacifica* and 22% to *S. dahurica*; *Peng 12158* A from Taiwan; dwarf shoot) and 45% probability (34% to *S dahurica* and 19% to *S. pacifica*; *Wilson 1695* K from Hubei Prov., China; robust shoot). Seven specimens of *S. decurrens* were assigned a posteriori to other species: 3 specimens to *S. dahurica* with 73%, 62%, and 49% probabilities, 2 specimens to *S. pacifica* with 78% and 44% probabilities, 1 specimen to *S. spithamaea* with 81% probability, and 1 specimen to *S. minutissima* with 68% probability (*Tsang 2448* A from Guangxi Prov., China; 44 cm tall shoot). Six of 8 specimens of the *S. litoralis* a priori group (75%) were assigned a posteriori to the *S. litoralis* group: 1 specimen with 83% probability, 3 specimens with 64-68% probability, 1 specimen with 50% probability, and 1 specimen with 44% probability. Two specimens of the *S. litoralis* a priori group were assigned to other species: 1 specimen to *S. leiocarpa* with 59% probability (38% to *S. litoralis*; *Bussotti s.n.* PI) and 1 specimen to *S. pacifica* with 48% probability (16% to S. litoralis, 11% to *S. virgaurea*, 11% to *S. decurrens*, and 5% to *S. dahurica*; Nouoli s.n. PI). Seventeen of 25 specimens of the *S. dahurica* a priori group (68%) were assigned a posteriori to the *S. dahurica* group: 3 specimens with 95-100% probability, 5 specimens with 83-89% probability, 2 specimens with 70-71% probability, 2 specimens with 66% and 60% probabilities, 4 specimens with 50-58% probability, and 1 specimen with 46% probability (40% to *S. decurrens*; 40% to *S. decurrens* and 11% *to S. pacifica*; *Konnikov-Galitsky 1218* MO from Zabaykasky Krai, eastern Russia). Eight specimens of the *S. dahurica* a priori group were assigned to other species: 4 specimens to *S. decurrens* with 77% probability (from Pakistan), 70% probability (from Nepal), 65% probability (from Pakistan) and 32% probability (32% to *S. dahurica*, 205 to *S. pacifica*, and 8% to S. kurilensis; from Kamchatka); 2 specimens to *S. pacifica* with 86% probability (from northeastern China) and 41% probability (26% to *S. kurilensis* and 23% to *S. decurrens*; Uzbekistan); 1 specimen to *S. macrophylla* with 52% probability, and 1 specimen to *spithamaea* with 31% probability (28% to *S. dahurica*, 27% to *S. kurilensis* and 13% to *S. virgaurea*); and 1 specimen to *S. macrophylla* with 52% probability (36% to *S. dahurica* and 7% to *S. spithamaea*; from India). Five of 9 specimens of the *S. pacifica* a priori group (56%) were assigned a posteriori to the *S. pacifica* group: 3 specimens with 91-100% probability, 1 specimen with 79% probability, and 1 specimen with 55% probability (33% to *S. decurrens* and 7% to *S. kurilensis*). Four specimens of the *S. pacifica* a priori group were assigned to other species: 2 specimens to *S. dahurica* with 82% probability and 53% probability; and 2 specimens to *S. decurrens* with 73% probability and 50% probability (49% to *S. pacifica*). Seven of 13 specimens of the *S. leiocarpa* a priori group (54%) were assigned a posteriori to the *S. leiocarpa* group: 3 specimens with 90-97% probability, 1 specimen with 84% probability, 2 specimens with 76% and 73% probabilities, and 1 specimen with 67% probability. Six specimens of the *S. leiocarpa* a priori group were assigned to other species: 3 specimens to *S. litoralis* with 91% probability, 73% probability, and 45% probability; and 2 specimens to *S. spithamaea* with 93% probability and 59% probability. Sixteen of the 31 specimens of the *S. virgaurea* a priori group (52%) were assigned a posteriori to the *S. virgaurea* group: 4 specimens with 90-95% probability, 1 specimen with 825 probability, 4 specimens with 72-74% probability, 2 specimens with 47% probability and 45% probability. Fifteen specimens of the *S. virgaurea* a priori group were assigned a posteriori to other

species: 3 specimens to *S. litoralis* with 93% probability, 88% probability, and 53% probability; 3 specimens to *S. kurilensis* with 72% probability, 59% probability and 45% probability); 2 specimens to *S. dahurica* with 85% probability and 30% probability; 2 specimens to *S. spithamaea* with 61% probability and 55% probability; 2 specimens to *S. decurrens* with 55% probability and 36% probability; and 1 specimen to *S. multiradiata* with 88% probability.

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of 13 a priori groups; a posteriori placements to groups in rows.

Group	***dahurica***	***decurrens***	***kurilensis***	***leiocarpa***	***litoralis***	***macrophylla***	***minutissima***	***multiradiata***	***pacifica***	***spithamaea***	***virgautea***	**% correct**
dahurica	17	4	0	0	0	1	0	0	2	1	0	68
decurrens	3	37	0	0	0	0	1	0	2	1	0	84
kurilensis	0	2	17	0	0	0	0	0	0	0	1	85
leicocarpa	1	0	0	7	3	0	0	0	0	2	0	54
litoralis	0	0	0	1	6	0	0	0	1	0	0	75
macrophylla	0	0	0	0	0	13	0	0	0	0	0	100
minutissima	0	0	0	0	0	0	13	0	0	0	0	100
multiradiata	0	0	0	0	0	0	1	15	0	0	1	88
pacifica	2	2	0	0	0	0	0	0	5	0	0	56
spithamaea	1	0	1	0	0	0	0	0	0	11	0	85
virgaurea	1	2	4	0	3	0	0	1	1	3	16	52
Totals	25	47	22	8	12	14	15	16	11	18	18	76

Jackknifed classification matrix

Group	***dahurica***	***decurrens***	***kurilensis***	***leiocarpa***	***litoralis***	***macrophylla***	***minutissima***	***multiradiata***	***pacifica***	***spithamaea***	***virgautea***	**% correct**
dahurica	13	5	1	0	0	1	0	0	4	1	0	52
decurrens	3	36	0	0	0	0	2	0	2	1	0	82
kurilensis	0	2	16	0	0	0	0	0	0	1	1	80
leicocarpa	1	0	0	6	4	0	0	0	0	2	0	46
litoralis	0	0	0	3	3	0	0	0	1	0	1	38
macrophylla	0	0	0	0	0	12	0	0	1	0	0	92
minutissima	0	0	0	0	0	0	13	0	0	0	0	100
multiradiata	0	0	0	0	0	0	1	15	0	0	1	88
pacifica	2	3	0	0	0	0	0	0	4	0	0	44
spithamaea	1	1	1	1	0	0	0	0	0	9	0	69
virgaurea	1	2	4	0	5	0	0	1	1	3	14	45
Totals	21	49	22	10	12	12	16	16	13	17	17	68

Two dimensional plots of CAN1 versus CAN2 and CAN1 versus CAN3 canonical scores for 206 specimens of *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. litoralis*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea,* and *S. virgaurea* plus 1 additional specimen of *S. horieana*, 5 specimens of *S. virgaurea*, and 5 specimens of *S. yokusaiana* only included a posteriori and are presented in Fig. 32. Eigenvalues on the first three axes were 2.736, 2.698, and 1.144.

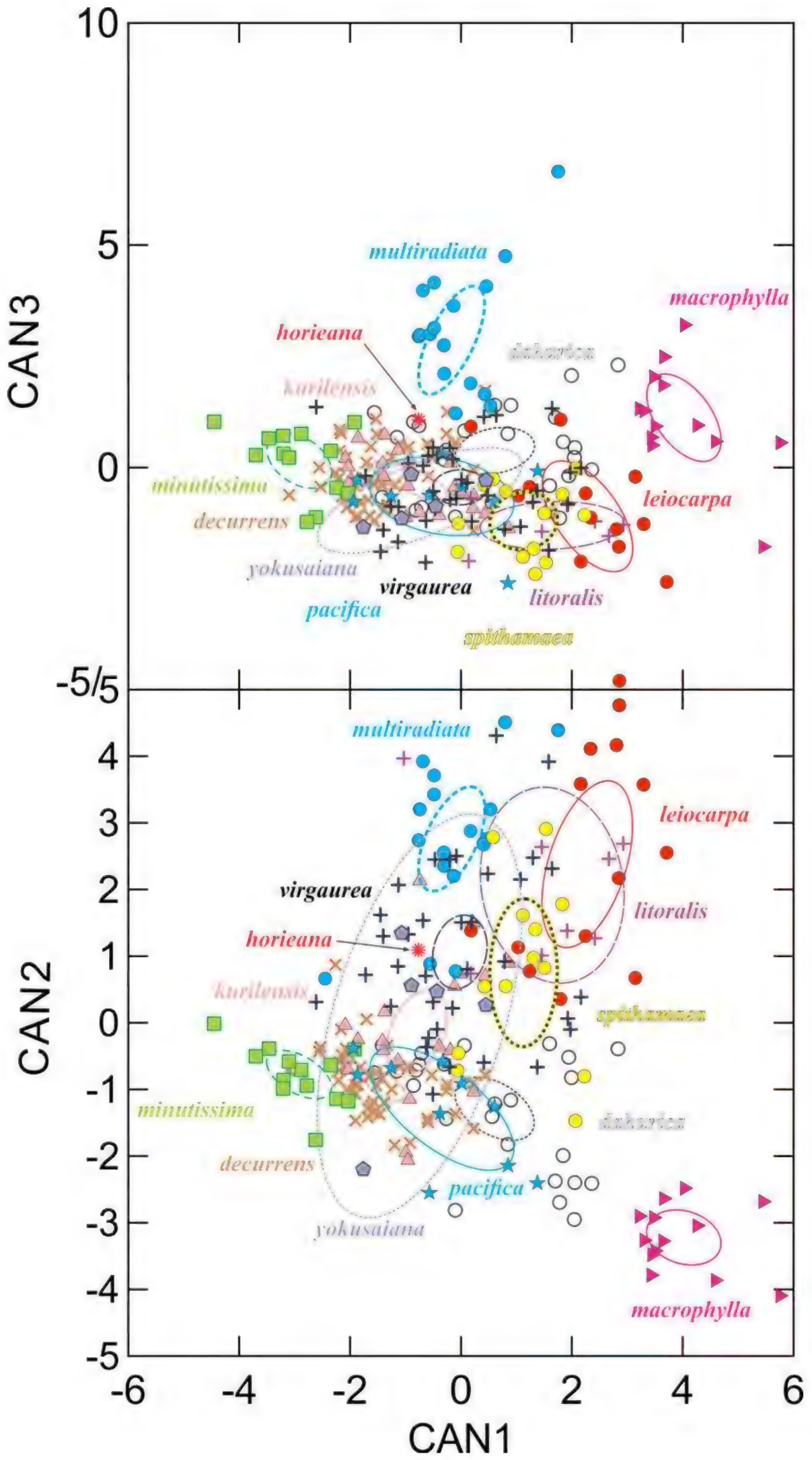

Figure 32. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 206 a priori specimens of species of *Solidago* ser. *Solidago, S. macrophylla*, and *S.* sect. *Multiradiata* and 11 a posteriori specimens based on a COMPLETE discriminant analysis using seven traits: *S. dahurica* (open black circles), *S. decurrens* (light brown ×s), *S. horieana* (red star burst), *S. leiocarpa* (red dots), *S. litoralis* (purple +s), *S. macrophylla* (magenta right-oriented triangles), *S. minutissima* (light green squares), S. multiradiata, *S. pacifica* (light blue stars), *S. spithamaea* (yellow dots), and *S. virgaurea* (black +s); 95% confidence limits indicated by ellipses.

Three higher level a priori groups analysis

The Pearson correlation matrix for traits of specimens of ser. *Macrophyllae*, sect. *Multiradiatae*, and ser. *Solidago* was the same as in the eleven species analysis reported above.

In the STEPWISE discriminant analysis of 216 specimens of three species level a priori eleven traits were selected and are listed in order of decreasing F-to-remove values: number of ray florets (62.08), mid leaf margin serrations (26.33), total number of disc floret ovary/fruit body hairs (24.05), mid series phyllary length (19.16), disc corolla lobe length (14.97), ray floret lamina length

(14.86), disc floret corolla length (8.71), ray floret pappus length (7.58), mid series phyllary width (7.01), involucre height (4.17), and mid stem leaf length (4.15). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 5. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between sect. *Multiradiatae* and ser. *Solidago* (40.103); the smallest separation was between ser. *Macrophyllae* and sect. *Multiradiatae* (29.317).

Table 5. Between groups F-matrix for the three higher level a priori groups analysis (df = 11 203).

Group	*Macrophyllae*	*Multiradiatae*
Multiradiatae	29.317	
S. ser. Solidago	32.560	40.103

Wilks' lambda = 0.1178 df = 11 2 213; Approx. F= 35.3061 df = 22 406 prob = 0.0000

In the Classificatory Discriminant Analysis of 216 specimens of the three higher level a priori groups (*Solidago ser. Macrophyllae*, *S.* sect. *Multiradiatae*, and *S.* ser. *Solidago*), percents of correct a posterori assignment to the same a priori group ranged from 95-100%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. All 13 specimens of the *S.* ser. *Macrophyllae* a priori group (100%) were assigned a posteriori into the *S.* ser. *Macrophyllae* group; all specimens with 100% probability. One hundred and fifty-nine of 160 specimens of the *S.* ser. *Solidago* a priori group (99%) were assigned a posteriori into the *S.* ser. *Solidago* group; 144 specimens with 94-100% probability, 4 specimens with 81-89% probability, 4 specimens with 72-78% probability, 3 specimens with 62-66% probability, 2 species with 55% and 53% probabilities. One specimen of the *S.* ser. *Solidago* a priori group was assigned to the ser. *Macrophyllae* group with 51% probability (49% probability to the *S.* ser. *Solidago*; *Nouoli s.n.* PI, a densely hairy *S. litoralis* shoot from Calambrone, Italy). Forty-one of 43 specimens of the *S.* sect. *Multiradiatae* a priori group (95%) were assigned a posteriori to the *S.* sect. *Multiradiatae* group: 38 specimens with 97-100 probability, 2 specimens with 89% and 84% probabilities, and 1 specimen with 58% probability. Two specimens of the *S.* sect. *Multiradiatae* a priori group were assigned to *S.* ser. *Solidago*: 1 specimen with 100% probability (*Hawthorn s.n.* WAT; a *S. multiradiata* collection from Churchill, Manitoba) and 1 specimen with 97% probability (*Semple et al. 11165* WAT; a *S. multiradiata* collection from Nahanni NPR, Northwest Territories).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 216 specimens of *Solidago ser. Macrophyllae*, *S.* sect. *Multiradiatae*, and *S.* ser. *Solidago* is presented in Fig. 33. Eigenvalues on the first two axes were 2.280 and 1.588.

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*Macrophyllae*	*Multiradiatae*	*Solidago*	% correct
Macrophyllae	13	0	0	100
Multiradiatae	0	41	2	95
Solidago	1	0	159	99
Totals	14	41	161	99

Jackknifed classification matrix

Group	*Macrophyllae*	*Multiradiatae*	*Solidago*	% correct
Macrophyllae	13	0	0	100
Multiradiatae	0	40	3	93
Solidago	4	1	155	97
Totals	17	41	158	96

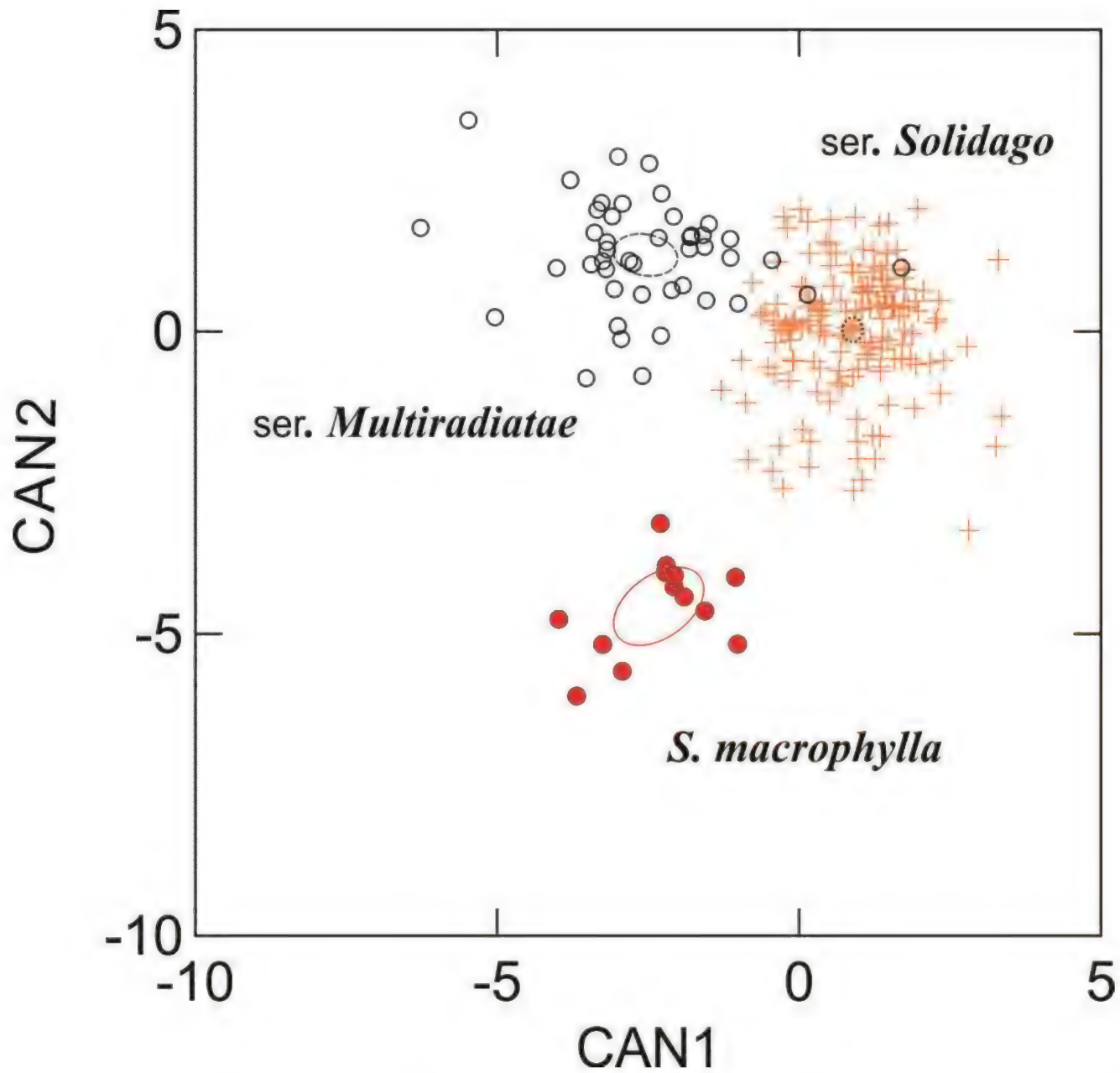

Figure 33. Plot of canonical scores (CAN1 vs CAN2) analysis for 216 specimens of *Solidago*: ser. *Macrophyllae* (red dots), sect. *Multiradiatae* (black circles), and ser. *Solidago* (light brown +s).

Three species level a priori groups analysis: *Solidago ser. Multiradiatae*

The Pearson correlation matrix for traits of specimens of three species of sect. *Multiradiatae*, (*S. leiocarpa*, *S. multiradiatae*, and *S. spithamaea*) included r > |0.7| for most pairs of basal and lower leaf traits and mid and upper leaf traits reducing the traits used to mid stem leaf length and number of serrations. Basal rosette leaves were often present but were not included in the discriminant analyses. Only two pairs of floral traits were highly correlated: 1) ray floret lamina length and ray floret pappus length and 2) ray floret pappus length and disc floret pappus length. Ray floret lamina length and disc floret pappus length were included in the STEPWISE analysis.

In the STEPWISE discriminant analysis of 43 specimens of three species level a priori groups in sect. *Multiradiatae*, (*S. leiocarpa*, *S. multiradiatae*, and *S. spithamaea*), the following seven traits were selected and are listed in order of decreasing F-to-remove values: mid series phyllary width 1 mm below apex (59.75), disc floret pappus length (23.73), mid series phyllary width (22.01), ray floret lamina width (15.55), number of mid stem leaf serrations (11.52), disc floret ovary/fruit body length (6.06), and mid series phyllary length (5.26). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 7. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. multiradiata* and *S. spithamaea* (91.016); the smallest separation was between *S. leiocarpa* and *S. spithamaea* (25.406).

Table 7. Between groups F-matrix for the four species level a priori groups analysis (df = 7 34).

Group	*leiocarpa*	*multiradiata*
multiradiata	59.787	
spithamaea	25.406	91.016

Wilks' lambda = 0.0087 df = 7 2 40; Approx. F= 47.3623 df = 14 68 prob = 0.0000

In the Classificatory Discriminant Analysis of 43 specimens of the three species level a priori groups (*S. leiocarpa*, *S. multiradiatae*, and *S. spithamaea*), percents of correct a posterori assignment to the same a priori group was 100% for all three groups with all specimens being placed in their appropriate groups with 100% probability. The Classification matrix and Jackknife classification matrix are presented in Table 8.

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*leiocarpa*	*multiradiata*	*spithamaea*	% correct
leiocarpa	13	0	0	100
multiradiata	0	17	0	100
spithamaea	0	0	13	100
Totals	13	17	13	100

Jackknifed classification matrix

Group	*leiocarpa*	*multiradiata*	*spithamaea*	% correct
leiocarpa	13	0	0	100
multiradiata	0	17	0	100
spithamaea	0	0	13	100
Totals	13	17	13	100

Two dimensional plot of CAN1 versus CAN2 canonical scores for 43 specimens of *Solidago leiocarpa*, *S. multiradiata*, and *S. spithamaea* is presented in Fig. 34. Eigenvalues on the first two axes were 20.430 and 4.394.

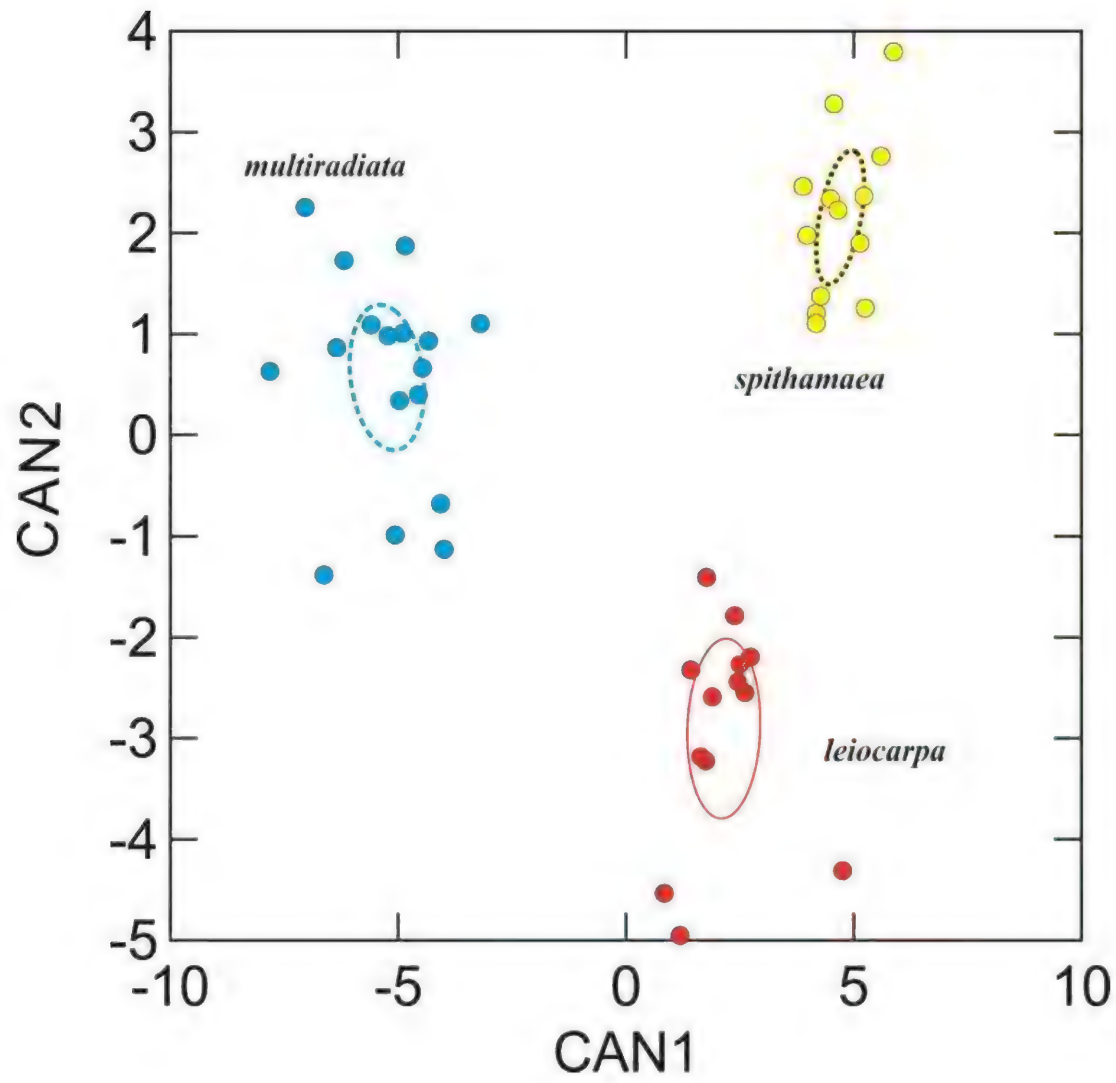

Figure 34. Plot of canonical scores (CAN1 vs CAN2) analysis for 43 specimens of *Solidago* sect. *Multiradiata*: *S. leiocarpa* (open blue stars), *S. multiradiata* (red circles), and *S. spithamaea* (yellow stars).

Seven species level a priori groups analysis: *Solidago* ser. *Solidago*

The Pearson correlation matrix yielded r > |0.7| that was similar to that for all taxa in the first analysis. Only mid stem leaf length and number of serrations were used in the analysis of ser. *Solidago*. Floral traits used were the same as those in the first analysis.

In the STEPWISE discriminant analysis of 150 specimens of seven species level a priori groups (*S. dahurica, S. decurrens, S. kurilensis, S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea* plus 1 additional specimen of *S. horieana*, 5 specimens of *S. virgaurea*, and 5 specimens of *S. yokusaiana* only included a posteriori), the following seven traits were selected and are listed in order of decreasing F-to-remove values: total number of disc floret ovary/fruit body hairs (33.96), disc floret pappus length (16.48), number of mid stem leaf serrations (8.92), mid stem leaf length (7.07), ray floret lamina width (4.92), mid series phyllary width (4.29), and involucre height (3.94). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. litoralis* and *S. minutissima* (49.417) and *S. litoralis* and *S. decurrens* (40.840); the smallest separations were between *S. decurrens* and *S. pacifica* (2.447) and *S. dahurica* and *S. pacifica* (3.997).

Table 9. Between groups F-matrix for the 7 a priori species groups analysis (df = 7 137).

Group	***dahurica***	***decurrens***	***kurilensis***	***litoralis***	***minutissima***	***pacifica***
decurrens	21.638					
kurilensis	22.783	17.379				
litoralis	21.245	40.840	32.690			
minutissima	38.000	13.741	17.092	49.417		
pacifica	3.997	2.447	8.536	22.811	14.905	
virgaurea	19.657	29.447	12.178	16.365	34.455	10.290

Wilks' lambda = 0.03297 df = 7 6 143; Approx. F= 16.4651 df = 42 646 prob = 0.0000

In the Classificatory Discriminant Analysis of 150 specimens of seven species level a priori groups (*S. dahurica, S. decurrens, S. kurilensis, S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea*) plus 12 additional specimens only included a posteriori of (1 specimen of *S. dahurica*; 1 specimen of *S. horieana*; 6 specimens of *S. virgaurea* from Estonia, South Kazakhstan, Pakistan, India, Nepal; and 5 specimens of *S. yokusaiana*), percents of correct a posteriori assignment to the same a priori group ranged from 56-100%. The Classification matrix and Jackknife classification matrix are presented in Table 10. Results are presented in order of decreasing percents of correct placement. Thirteen of the 13 specimens of the *S. minutissima* a priori group (100%) were assigned a posteriori into the *S. minutissima* group with 93-100% probability. Eight of 8 specimens of the *S. litoralis* a priori group (100%) were assigned a posteriori into the *S. litoralis* group with 99-100% probability. Thirty-five of the 44 specimens of the *S. decurrens* a priori group (80%) were assigned a posteriori to the *S. decurrens* group: 2 specimens with 93% and 91% probabilities, 10 specimens with 80-89% probability, 11 specimens with 71-78% probability, 7 specimens with 61-69% probability, and 4 specimens with 59% probability (33% to *S. pacifica*; *Miki et al. 81* MO from Honshu, Japan), 53% probability (42% to *S. pacifica*; *Feng 12731* A from Yunnan Prov., China), 50% probability (25% to *S. pacifica*, 23% to *S. dahurica*; *Peng 12158* A from Taiwan), and 50% probability (29% to *S. virgaurea, 21% to S. dahurica*; *Clarke 18650* BM from India; holotype/lectotype of *S. virgaurea* var. *glabriuscula* Clark). Nine specimens of the *S. decurrens* a priori group were assigned to other species: 6 specimens to *S. pacifica* with 88% probability (*Sino-Amer. Exped. 2016* A from Hubei Prov., China), 72% probability (26% to *S. decurrens*; *Sino-Amer. Exped. 1257* A from Hubei Prov. China), 54% probability (22% to *S. decurrens*; *Togast 791* MO from Miyagi, Japan), 50% probability (41% to *S. decurrens*; *Hooker & Thomson s.n.* K from Khasia Hills, Meghalaya Prad., India), 49% probability (30% to *S. decurrens*, 17% to *S. dahurica*; *Niu 91401* MO from Jiangxi Prov., China), and 43% probability (42% to *S. decurrens*, 13% *S. dahurica*; *Furuse 1875* K from Okinawa Pref., Japan); 1 specimen to *S. dahurica* with 70% probability (20% to *S. minutissima*; *Wilson 1695* K from Hubei Prov., China); 1 specimen to *S. minutissima* with 54% probability (45% to *S. decurrens*; *Tsang 24487* A from Guangxi Prov., China); and 1 specimen to *S. kurilensis* with 44% probability (30% to *S. decurrens* and 25% to *S. pacifica*; *Boufford et al. 25836* A from South Korea). Sixteen of 20 specimens of the *S. kurilensis* priori group (80%) were assigned a posteriori to the *S. kurilensis* group: 9 specimens with 90-100% probability, 6 specimens with 81-87% probability, and 1 specimen with 69% probability. Four specimens of the *S. kurilensis* a priori group were assigned to other species: 1 specimens to *S. virgaurea* with 97% probability (*Konta 19657* A from Aomori Pref., Japan); and 3 specimens to *S. decurrens* with 84% probability (10% to *S. virgaurea*; *Kitamura s.n.* KYO from Hokkaido Pref., Japan), 60% probability (18% to *S. virgaurea*, 17% to *S. kurilensis*; *Kurosaki 6416* KYO from Hokkaido Pref., Japan), and 38% probability (34% to *S. kurilensis*, 24% to *S. virgaurea*;

Staff of Bot. Gard. Tohoku U. 72905 MO from Ogachi-gun, Akita Pref., Japan). Nineteen of 25 specimens of the *S. dahurica* a priori group (76%) were assigned a posteriori to the *S. dahurica* group: 11 specimens with 90-99% probability, 4 specimens with 62-69% probability, 1 specimen with 50% probability (36% to *S. kurilensis*, 11% to *S. virgaurea*; *Russell 1729* BM from Jammu and Kashmir Prad., India), and 3 specimens with 44% probability (40% to *S. pacifica*, 11% to *S. decurrens*; *Stewart 13510* MO from Kashmir, Pakistan), 44% probability (35% to *S. virgaurea*, 20% to *S. kurilensis*; *Abel 110* BM from northeastern Pakistan; Fig. 6I), and 39% probability (32% to *S. decurrens*, 28% to *S. virgaurea*; *Eyerdam s.n.* MO from Kamchatka, Russia). Six specimens of the *S. dahurica* a priori group were assigned a posteriori to other species: 1 to *S. virgaurea* with 73% probability (24% to *S. dahurica*; *Yang 86-0886* WAT from Xinjiang Prov., China); and 5 specimens to *S. pacifica* with 55% probability (24% to *S. dahurica*, 17% to *S. decurrens*; *Kopronovich s.n.* MO from "Manchuria", China), 48% probability (46% to *S. dahurica*; *Navnova 4493* MO from Ilansky, Krasnoyjarsk Krai, Russia), 47% probability (35% to *S. dahurica*, 18% to *S. decurrens*; *Stewart s.n.* GH from Kamchatka, Russia), and 38% probability (32% to *S. dahurica*, 17% to *S. decurrens*, 13% to *S. virgaurea*; *Tabata et al. 13668* A from Nepal). Twenty of 31 specimens of the *S. virgaurea* a priori group (65%) were assigned a posteriori to the *S. virgaurea* group: 11 specimens with 91-100% probability, 3 specimens with 82-88% probability, 2 specimens with 78% and 70% probability, 2 specimens with 58% probability (41% to *S. kurilensis*; *King 11965* MO from Mont Ventoux, Dept. Vaucluse, France) and 56% probability (44% to *S. litoralis*; *Alm 2399* MO from Lake Tornetrask Dist., Switzerland), and 2 specimens with 49% probability (42% to *S. kurilensis*; *Parlatore s.n.* MO from Terni Prov., Italy) and 39% probability (30% to *S. pacifica*, 22% to *S. decurrens*, 8% to *S. kurilensis*; *Pankakoski s.n.* MO from Tyrväntö, Finland). Six of 9 specimens of the *S. pacifica* a priori group (56%) plus 1 specimen included a posteriori were assigned a posteriori to the *S. pacific* group: 3 specimens with 73-77% probability, 2 specimens with 56% probability (25% to *S. dahurica*, 16% to S. kurilensis; *Tonghua Team 152* PE from Jilin Prov., China) and 54% probability (27% to *S. decurrens*, 19% to *S. dahurica*; *Wang 563* PE from from Jilin Prov., China), and 3 specimens with 49% probability (43% to *S. dahurica*, 7% *S. decurrens*; *Wang 408* PE from Heilongjiang Prov., China; Fig. 17), and 43% probability (33% to *S. kurilensis*, 21% to *S. decurrens*; *Komarov 1499* K from "Manchuria", China). Four specimens of the *S. pacifica* a priori group were assigned a posteriori to other species; 3 specimens to *S. decurrens* with 85% probability (14% *S. pacifica*; *Skvortsov s.n.* MO from vicinity of Vladivostok, Russia), 56% probability (44% to *S. pacifica*; *Wan & Chow 81116* MO from Changbaishan, Jilin Prov., China), and 43% probability (42% to *S. pacifica*; *Maack s.n.* GH near Amur River, "Manuchuria", China); and 1 specimen to *S. dahurica* with 74% probability (23% to *S. pacifica*; *Wan & Chow 81116* BM from Changbaishan, Jilin Prov., China).

Ten additional specimens were not assigned to an a priori group in the analysis and were only included a posteriori in the Classificatory Discriminant Analysis. One specimen of *S. horieana* (*Horrie 1107* TNS) was assigned a posteriori to *S. kurilensis* with 75% probability (21% to *S. virgaurea*). Five specimens of putative *S. virgaurea* from central Asia were assigned a posteriori as follows: 3 specimens were assigned a posteriori to *S. virgaurea* with 73% probability (23% to *S. dahurica*; *Stainton et al. 8160* BM from Nepal), 55% probability (37% *S. dahurica*; *Thompson s.n.* GH from Hamachal Pradesh, India), and 47% probability (21% to *S. kurilensis*, 16% to *S. pacifica* and 10% to *S. dahurica*; *Tabata et al. 20280* A from Nepal); 1 specimen was assigned a posteriori to *S. litoralis* with 94% probability (*FeSissaw s.n.* K from South Kazakhstan); and 1 specimen was assigned a posteriori to *S. dahurica* with 67% probability (30% to *S. virgaurea*; *Polunin, Sykes & Williams 2610* BM from Nepal). Four specimens of the morphologically distinct *S. yokusaiana* were assigned a posteriori as follows: 1 specimen to *S. kurilensis* with 92% probability (*Tanaka s.n.* {*Beaudry* 58-320-2 MT} cultivated from seed, Jardin botanique, Montréal, Québec; originally from Huzo Canyon, near Kyoto, Japan); 1 specimen to *S. virgaurea* with 85% probability (*Tanaka s.n.*{*Beaudry* 58-320-1 MT} cult. F1, Montréal, Québec), 1 specimen to *S. dahurica* with 74%

probability (*Kimura & Sugaya s.n.* A from Yamagata Pref., Japan), and 1 specimen to *S. minutissima* with 48% probability (31% to *S. kurilensis*, 12% to *S. virgaurea*; Shiota *997* GH from from Gifu Pref., Japan).

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	***dahurica***	***decurrens***	***kurilensis***	***litoralis***	***minutissima***	***pacifica***	***virgaurea***	**% correct**
dahurica	19	0	0	0	0	5	1	76
decurrens	1	35	1	0	1	6	0	80
kurilensis	0	3	16	0	0	0	1	80
litoralis	0	0	0	8	0	0	0	100
minutissima	0	0	0	0	13	0	0	100
pacifica	1	3	0	0	0	5	0	56
virgaurea	5	1	3	2	0	0	20	65
Totals	26	42	20	10	14	10	22	77

Jackknifed classification matrix

Group	***dahurica***	***decurrens***	***kurilensis***	***litoralis***	***minutissima***	***pacifica***	***virgaurea***	**% correct**
dahurica	15	1	1	0	0	6	2	76
decurrens	1	35	1	0	1	6	0	80
kurilensis	0	3	16	0	0	0	1	80
litoralis	0	1	0	7	0	0	0	100
minutissima	0	0	0	0	13	0	0	100
pacifica	2	3	1	0	0	3	0	56
virgaurea	5	1	4	3	0	1	17	65
Totals	23	44	23	10	14	16	20	77

Two dimensional plots of CAN1 versus CAN2 and CAN1 versus CAN3 canonical scores for 150 specimens of *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis, S. minutissima*, *S. pacifica*, and *S. virgaurea* plus 1 additional specimen of *S. horieana*, 5 specimens of *S. virgaurea*, and 5 specimens of *S. yokusaiana* only included a posteriori and are presented in Fig. 35. Eigenvalues on the first three axes were 3.765, 1.532, and 0.692.

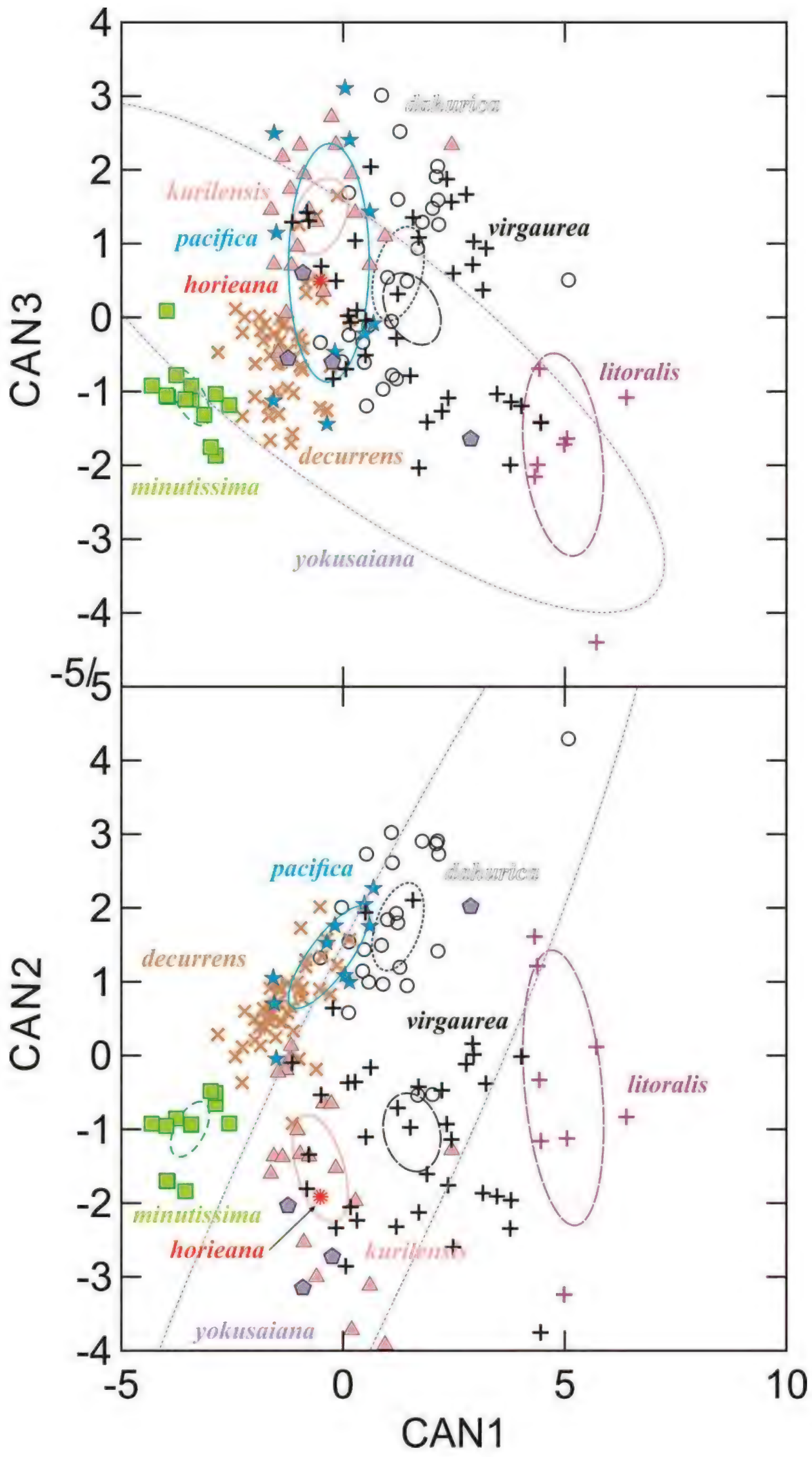

Figure 35. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 150 a priori specimens of species of *Solidago* ser. *Solidago,* and 11 a posteriori specimens *S. horieana*, *S. virgaurea* and *S. yokusaiana* based on a Stepwise discriminant analysis using seven traits: *S. dahurica* (open black circles), *S. decurrens* (light brown ×s), *S. horieana* (red star burst), *S. litoralis* (purple +s), *S. minutissima* (light green squares), *S. pacifica* (light blue stars), *S. virgaurea* (black +s), and *S. yokusaiana* (lavender pentagons); 95% confidence limits indicated by ellipses.

Two species level a priori groups analysis of *S. litoralis* and *S. virgaurea*

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length and the numbers of serrations of mid and upper stem leaves. Multiple pairs of floret traits were correlated: involucre height correlated highly with mid series phyllary length and width, lengths of ray and disc floret pappi, and length of disc corolla, mid stem phyllary width correlated with length of ray and disc floret pappi, number of ray florets correlated with length, of ray and disc floret pappi, ray floret pappus length correlated with disc floret pappus length, and disc floret corolla length correlated with disc floret pappus length. Involucre height, numbers of ray and disc florets, ray floret lamina length and width, disc floret corolla and lobe lengths and total number of hairs on the disc floret ovary/cypsela body were included in the analysis.

In the STEPWISE discriminant analysis of 38 specimens of *Solidago litoralis* and *S. virgaurea*, one trait was selected in a STEPWISE analysis and is listed with F-to-remove value in parentheses: involucre height (17.26). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0002 that the null hypothesis was true. *Solidago litoralis* and *S. virgaurea* had an F-to separate value of 17.259 (Wilks' lambda =0.29888 df = 1 1 36; Approx. F= 17.259 df = 1 362 prob = 0.0002).

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori group were 86% for *S. litoralis* and 84% for *S. virgaurea*. The Classification matrix and Jackknife classification matrix are presented in Table 11. Six of 7 specimens of *S. litoralis* (86%) were assigned a posteriori to the *S. litoralis* group: 2 specimens with 91-95% probability, 2 specimens with 87% probability, and 2 specimens with 77% and 71% probabilities. One specimen of the *S. litoralis* a priori group was assigned to *S. virgaurea* with 72% probability (*Savi s.n.* GH; stem and leaves densely hairy). Twenty-six of the 31 specimens of *S. virgaurea* (84%) plus 1 additional specimen included a posteriori were assigned a posteriori to the *S. virgaurea* group: 10 specimens with with 93-100% probability including 3 specimens from Italy, 5 specimens with 82-89% probability, 7 specimens with 70-79% probability, 1 specimen with 66% probability, and 3 specimens with 59% probability (*Kamavesh s.n.* MT from Georgia), 55% probability (Brandis 2846 A from Bosnia), and 52% probability (*Skvortsov s.n.* MO from near Moscow, Russia). Five specimens of the *S. virgaurea* a priori group were assigned a posteriori to *S. litoralis* with 86% probability (*Shlyakova 62-2* MT from Murmansk Oblast, Russia), 79% probability (*Davis 50753* BM from Morocco), 79% probability (*Ollgaard s.n.* MO from Denmark), 69% probability (*Alm 2399* GH from Switzerland), and 64% probability (*Davis 21097* MO from northeastern Turkey); none of these collections had densely hairy lower to mid stems and leaves.

Frequencies of CAN1 canonical scores for specimens of *S. litoralis* and *S. virgaurea* are presented in histograms in Fig. 36. The eigen value on the first axis was 0.479.

Table 11. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*litoralis*	*virgaurea*	% correct
litoralis	6	1	86
virgaurea	5	26	84
Totals	11	27	84

Jackknifed classification matrix

Group	*litoralis*	*virgaurea*	% correct
litoralis	6	1	86
virgaurea	5	26	84
Totals	11	27	84

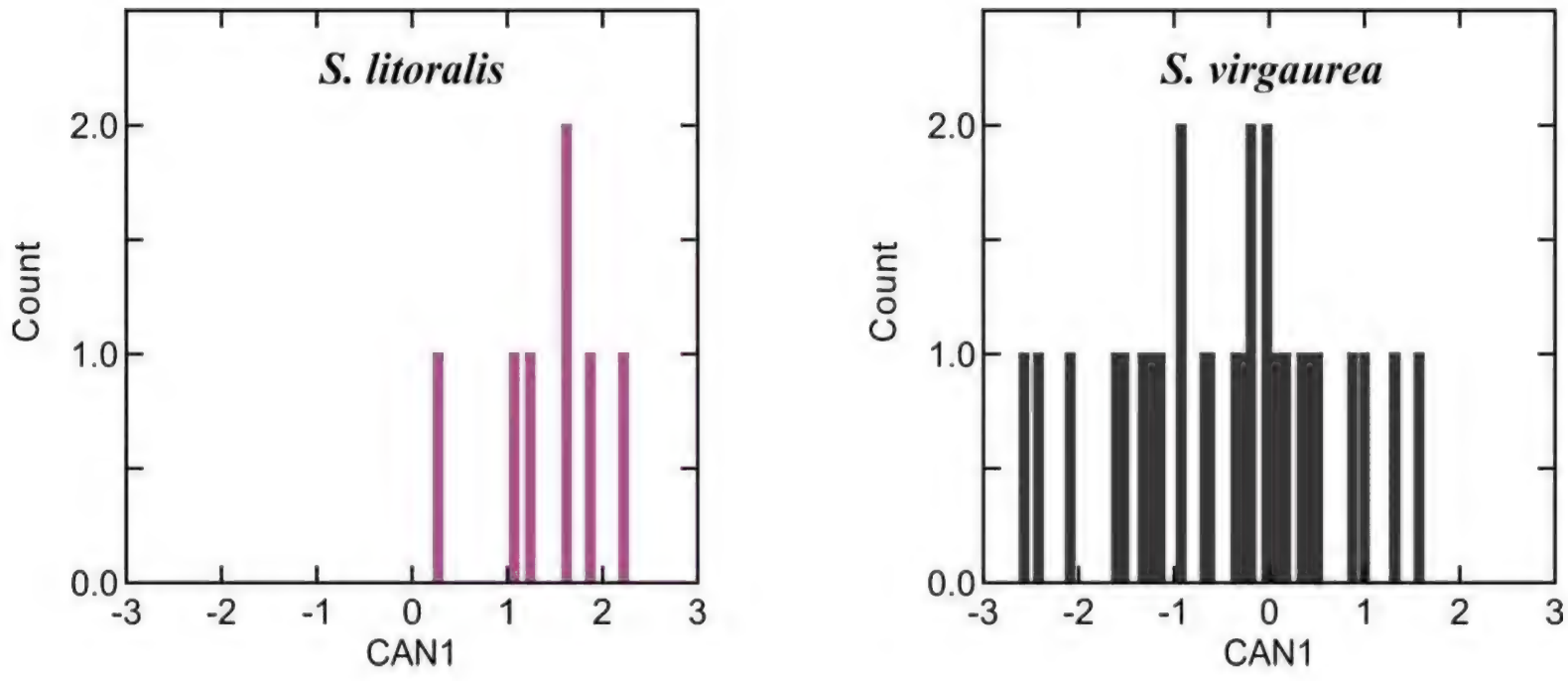

Figure. 36. Histograms of CAN1 canonical scores for 38 specimens of *S. litoralis* (left) and *S. virgaurea* (right).

Three species level a priori groups analysis of *S. dahurica*, *S. decurrens*, and *S. virgaurea*

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number used to mid stem leaf length and the numbers of serrations of mid and upper stem leaves. Three pairs of floret traits were correlated: involucre height and disc floret pappus length, ray floret lamina length and disc floret pappus length, and disc floret corolla length and disc floret pappus length. Disc floret pappus length was not included while the other three traits were along with all other floral traits.

In the STEPWISE discriminant analysis of 100 specimens of three species level a priori groups (*Solidago dahurica*, *S. decurrens*, and *S. virgaurea*) the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret ovary/furit body total number of hairs (95.43), involucre height (14.06),), ray floret lamina length (12.29), ray floret lamina width (9.93), and number of mid stem leaf margin serrations (8.31). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 12. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation were between *S. decurrens* and *S. virgaurea* (47.459) and the smaller separations were between *S. dahurica* and *S. decurrens* (25.163) and *S. dahurica* and *S. virgaurea* (27.639).

Table 12. Between groups F-matrix for the four species level a priori groups analysis (df = 5 97).

Group	*dahurica*	*decurrens*
decurrens	25.163	
virgaurea	27.639	47.459

Wilks' lambda = 0.1323 df = 5 2 97; Approx. F= 32.5293 df = 10 186 prob = 0.0000

In the Classificatory Discriminant Analysis of 100 specimens of the three species level a priori groups (*Solidago dahurica*, *S. decurrens*, and *S. virgaurea*) plus 6 specimens only included a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 84-98%. The Classification matrix and Jackknife classification matrix are presented in Table 13. Forty-three of the 44 specimens of the *S. decurrens* a priori group (98%) were assigned a posteriori into the *S. decurrens* group; 33 specimens with 90-100% probability, 5 specimens with 80-85% probability, 1 specimen with 72% probability, 1 specimen with 62% probability, and 3 specimens with 59% probability (41% to *S. dahurica*; *Peng 12158* A from Taiwan), 57% probability (43% to *S. dahurica*; *Niu 91401* MO from Jiangxi Prov., China), and 49% probability (49% to *S. dahurica*; *Wilson 1695* K from Hubei Prov., China). One specimen of the *S. decurrens* a priori group was assigned a posteriori to *S. dahurica* with 57% (38% to *S. decurrens*; *Tsang 20773* A from Guangdong Prov., China). Twenty-seven of 31 specimens of the *S. virgaurea* a priori group (87%) plus 6 specimens only included a posteriori were assigned a posteriori to *S. virgaurea*: 23 specimens with 90-100% probability plus 1 specimen from Nepal with 98% probability and 1 specimen from southern Kyrgystan with 97% probability (assigned a priori to *S. dahurica* but having an atypically hairy cypsela body, 1 specimen with 87% probability plus 1 specimen from Nepal included a posteriori with 81% probability, 1 specimen with 79% probability plus 1 specimen from Nepal with 73%, 1 specimen with 62% probability, and 1 specimen with 53% probability (47% to *S. dahurica*; *Skvortsov s.n.* MO from near Golitsyno, Moscow Oblast, Russia; cypsela body sparsely but evenly hairy). Four specimens of the *S. virgaurea* a priori group plus one specimen include a posteriori were assigned a posteriori to other species: 3 specimens to *S. dahurica* with 97% probability (*anon. 3947* MO of unknown provenance within the old USSR, if Asian than likely *S. dahurica*; only 5-8 few hairs on cypselae), 85% probability (*Alm & Smith 597* MO from Switzerland; only 10-15 hairs on cypselae), and 64% probability (*Karjagin s.n.* A from Azerbaijan; 14-26 hairs mostly distal on cypselae); 1 specimen included a priori and 1 specimen only included a posteriori were assigned to *S. decurrens* with 95% probability (*Kerner 3768* MO from Austria; 6-10 hairs on cypselae) and 86% probability (*Skvortsov et al s.n.* MO from Estonia; moderately evenly hairy cypselae). Twenty-one of 25 specimens of the *S. dahurica* a priori group (84%) were assigned a posteriori to the *S. dahurica* group: 14 specimens with 96-100% probability, 4 specimens with 80-83% probability, 2 specimens with 79% and 74% probabilities, and 1 specimen with 52% probability (*Konrokovits s.n.* MO from "Manchuria"; 5-12 hairs distal on cypselae). Four specimens of the *S. dahurica* a priori group were assigned to other species: 2 specimens to *S. virgaurea* with 93% probability (*Yang 86-0886* WAT from western Xinjiang Prov., China; 44-50 hairs on distal half of cypselae) and 91% probability (*Abel 110* BM from northeastern Pakistan; 45-50 hairs either mostly distal to on entire cypselae; Fig. 6I); 2 specimens to *S. decurrens* with 74% probability (*Ikonnikov-Galitsky 1218* A from Zabaykasky Krai, Russia; 10-16 distal hairs on cypselae) and 64% probability (*Stewart s.n.* GH from Kamchatka; 0-4 distal hairs on cypselae).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 106 specimens of *Solidago dahurica*, *S. decurrens*, and *S. virgaurea* are presented in Fig. 37. One additional specimen of *S. virgaurea* from Europe, 2 additional specimens of *S. dahurica* from Kyrgystan and Nepal, and 3 additional specimens of *S. virgaurea* from Nepal and Pakistan are included in the plot. Eigenvalues on the first two axes were 2.5222 and 1.128.

Table 13. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*dahurica*	*decurrens*	*virgaurea*	% correct
dahurica	21	2	2	84
decurrens	1	43	0	98
virgaurea	3	1	27	87
Totals	25	46	29	91

Jackknifed classification matrix

Group	*dahurica*	*decurrens*	*virgaurea*	% correct
dahurica	20	2	2	80
decurrens	2	42	0	95
virgaurea	4	1	26	84
Totals	26	46	28	88

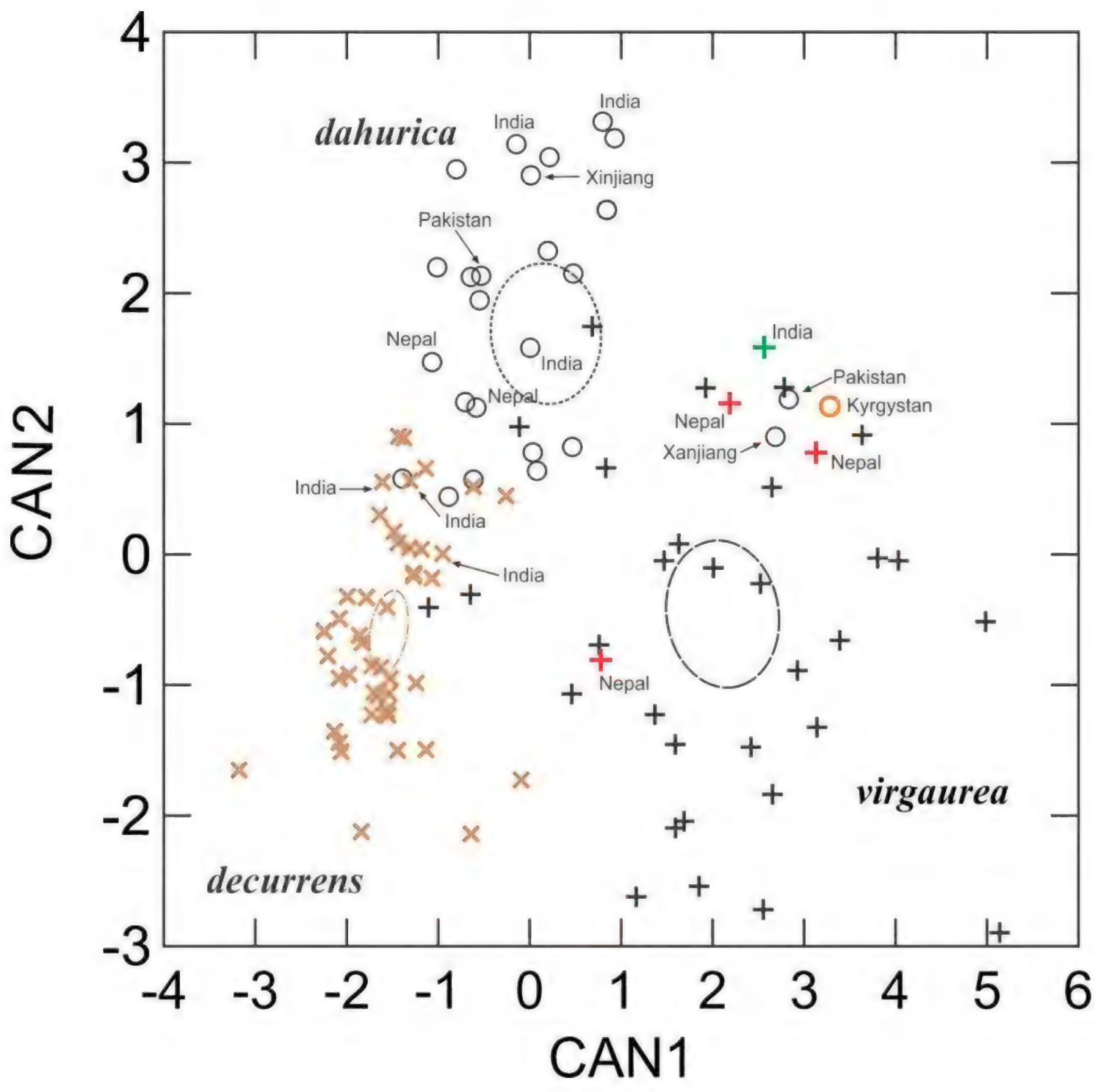

Figure 37. Plot of canonical scores (CAN1 vs CAN2) analysis for 106 specimens of *Solidago* ser. *Solidago*: *S. dahurica* (open black circles included a priori; orange circle include a posteriori), *S. decurrens* (light brown ×s), and *S. virgaurea* (black +s included a priori, red and green +s included a posteriori); source locations of some collections are also indicated.

Three species level a priori groups analysis of *S. decurrens*, *S. kurilensis* and *S. minutissima*

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number used to mid stem leaf length and the number of serrations of upper stem leaves. Three pairs of floret traits were correlated: involucre height and disc floret pappus length, ray floret pappus length and disc floret corolla lobe length, and disc floret corolla lob length and disc floret pappus length. Disc floret pappus length and disc floret lobe length were not included. Involucre height and ray floret pappus length were included along with all other floral traits.

In the STEPWISE discriminant analysis of 100 specimens of three species level a priori groups (*Solidago decurrens*, *S. kurilensis,* and *S. minutissima*), the following six traits were selected and are listed in order of decreasing F-to-remove values: disc floret ovary/fruit body total number of hairs (20.21), number of upper stem leaf serrations (15.23), mid stem leaf length (10.74), disc corolla length (9.58), involucre height (9.46), and mid series phyllary width 1 mm below apex (7.95). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 14. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. decurrens* and *S. kurilensis* (38.629); the smaller separation was between *S. decurrens* and *S. minutissima* (27.689).

Table 14. Between groups F-matrix for the four species level a priori groups analysis (df = 65 69).

Group	*decurrens*	*kurilensis*
kurilensis	38.629	
minutissima	27.689	31.432

Wilks' lambda = 0.0678 df = 6 2 74; Approx. F= 32.6722 df = 12 138 prob = 0.0000

In the Classificatory Discriminant Analysis of 77 specimens of the three species level a priori groups (*Solidago decurrens*, *S. kurilensis*, and *S. minutissima*) plus 1 specimen of *S. horieana* and 5 specimens of *S. yokusaiana* only included a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 85-100%. The Classification matrix and Jackknife classification matrix are presented in Table 15. All 44 specimens of the *S. decurrens* a priori group (100%) were assigned a posteriori into the *S. decurrens* group; 42 specimens with 94-100% probability, 1 specimen with 83% probability, and 1 specimen with 78% probability. All 13 specimens of the *S. minutissima* a priori group (100%) were assigned a posteriori to the *S. minutissima* group: 12 specimens with 96-100% probability and 1 specimen with 82% probability. Seventeen of 20 specimens of the *S. kurilensis* a priori group (85%) were assigned a posteriori to the *S. kurilensis* group: 16 specimens with 96-100% probability and 1 specimen with 86% probability. The holotype specimen of *S nipponica* (*Horie 1524* KYO) and the two shoots on the collection from Iturup Is., Kuril Arch., Russia were included among the specimens assigned a posteriori to *S. kurilensis* with 100% probability. Three specimens of the *S. kurilensis* a priori group were assigned a posteriori to *S. decurrens* with 91% probability (*Murata 6483* KYO from Sado Is., Niigata Pref., Japan), 83% probability (*Kitamura s.n.* KYO from Hakodate, Hokkaido Pref., Japan), and 55% probability (44% to *S. kurilensis*; *Staff of Bot. Gard. Tohoku U. 72905* MO from Ogachi-gun, Akita Pref., Japan); all three plants had rounded corymbiform inflorescences or truncate lower stem leaves typical of *S. kurilensis*). Six additional specimens were included a posteriori in the analysis. One specimen of *S. horieana* (*Horie s.n.* TNS from Kamikawa, Hokkaido Pref., Japan) was assigned to *S. kurilensis* with 100% probability, although leaf and inflorescence traits did not fit into *S. kuriensis*. Five specimens of *S. yokusaiana* were assigned a posteriori to three different species: 2 specimens to *S. kurilensis* with

100% probability and 99% probability (*Tanaka cult by Beaudry 58-320-2* MT originally from Hozu Canyon near Kyoto, Japan), 1 specimen to *S. decurrens* with 100% (*Kimura & Sugaya s.n.* A from Yamagata Pref., Japan; Fig. 19), and 2 specimens to *S. minutissima* with 100% probability (*Furuse 1864* K from Kunigami Dist., Okinawa Pref., Japan) and 58% probability (38% to *S. kurilensis*; *Shiota 997* GH from Mino Dist., Gifu Pref., Japan).

Table 15. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*decurrens*	*kurilensis*	*minutissima*	% correct
decurrens	44	0	0	100
kurilensis	3	17	0	85
minutissima	0	0	13	100
Totals	47	17	13	96

Jackknifed classification matrix

Group	*decurrens*	*kurilensis*	*minutissima*	% correct
decurrens	44	0	0	100
kurilensis	3	17	0	85
minutissima	0	0	13	100
Totals	47	17	13	96

A two dimensional plot of CAN1 versus CAN2 canonical scores for 77 specimens of *Solidago decurrens* (var. *decurrens* and var. *insularis* treated a priori as a single groups, but shown by different colored symbols in diagram), *S. kurilensis*, and *S. minutissima* are presented in Fig. 38. One additional specimen of *S. horienana* and 5 additional specimens of *S. yokusaiana* included a posteriori are shown in the plot. Eigenvalues on the first two axes were 3.368 and 2.378.

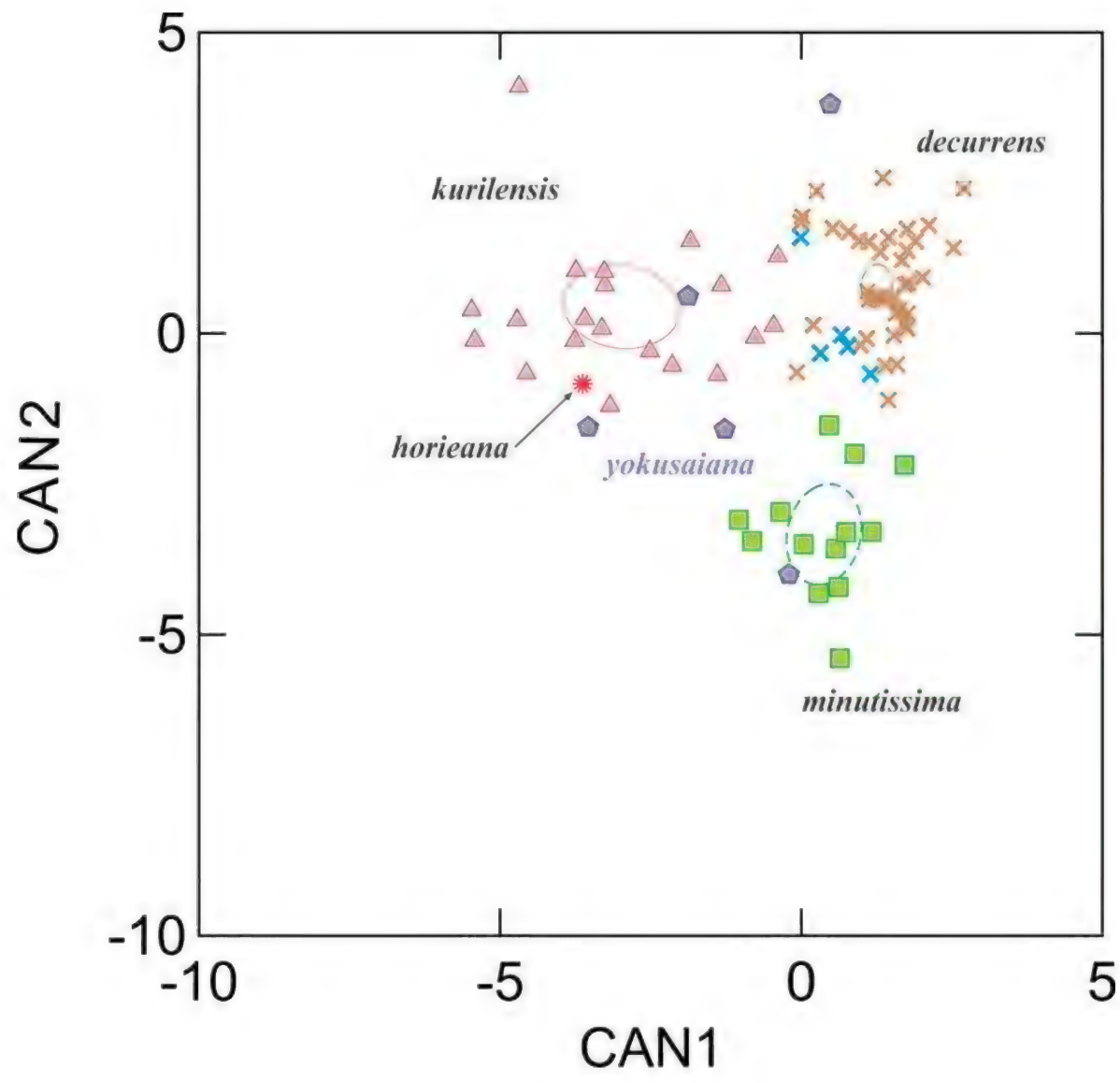

Figure 38. Plot of canonical scores (CAN1 vs CAN2) analysis for 77 specimens of *Solidago* ser. *Solidago* from eastern Asia: *S. decurrens* (var. decurrens are light brown ×s; var. *insularis* are blue ×s; 95% confidence ellipse includes a specimens of species), *S. kurilensis* (pink triangles), and S. minutissima (green squares) posteriori); specimens of S. horieana (red star burst) and *S. yokusaiana* (lavender pentagons) included a posteriori.

DISCUSSION

The results of the multivariate analyses provide support for recognizing the following species: *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea* in ser. *Solidago*, *S. macrophylla* in ser. *Macrophyllae*, and *S. leiocarpa*, *S. multiradiata*, and *S. spithamaea* in sect. *Multiradiatae*. *Solidago nippponica* was found to be the same taxon as *S. kurilensis* and thus belongs in synonymy under the older name. Although data were limited for some taxa in ser. *Solidago* the following taxa are also recognized: *S. decurrens* var. *insulars*, *S. horieana*, and *S. yokusaiana*. Just the digital image of the holotype collection of *Solidago virgaurea* var. *praeflorens* was available during this study, but this also appears to be an island arch race and is treated here as *Solidago decurrens* var. *praeflorens*.

The results of the ser. *Macrophyllae*, ser. *Solidago* and sect. *Multiradiatae* analysis indicate that the latter group is more morphologically distant from ser. *Solidago* than is ser. *Macrophyllae*. *Solidago macrophylla* is more similar to taxa in ser. *Solidago* than is *S. multiradiata*. This contradicts the results of the RFLP cp DNA-based study by Zhang (1996; Fig. 1 in Semple et al. 1999), which we conclude was the result of homoplasies between cpDNA fragments of *S. multiradiata* and *S. virgaurea*. Different mutations yielded approximately similar molecule weight fragments with the target DNA location at different positions within the fragments. Polygenomic sampling of the entire genome yields more historically accurate results (Beck et al. in prep.).

Further work is needed to determine if *Solidago virgaurea* sensu stricto should be split into species and varieties. At least 62 different names and combinations have been proposed for European variants of *S. virgaurea*. Most of these are undoubtedly just early published names that belong in synonymy under *S. virgaurea* var. *virgaurea*, if other varieties are recognized. Proposals to treat dwarf plants as distinct varieties, subspecies, or separate species are based on either geographically narrowly limited samples (e.g., Kiełtyk & Mirek 2014) or are really just alpha level taxonomic proposals that require much more work to document the distinctiveness of the proposed taxon. Based on how taxa of the genus *Solidago* in North America have apparently rapidly diverged, it seems reasonable to assume that some of the proposed names for European taxa occurring in isolated mountain ranges or distinct habitats might warrant some level of taxonomic recognition within *S. virgaurea*. In the analyses, *S. virgaurea* was not strongly supported and generally fell among the taxa with the lower levels of correct a posteriori placement. This is likely in part the result of significant emphasis being placed on the total number of ovary/cypselae body hairs, which varies more in *S. virgaurea* than any other taxon. In all cases, regardless of the number of hairs, individuals of *S. virgaurea* had some hairs covering the entire cypsela body, evenly in most cases and sometimes with more hairs distally than proximally. The results of the analyses indicate that *S. virgaurea* occurs in Europe and adjacent mountains in Morocco in North Africa and eastern Turkey in northwestern Asia. A gap in the distribution appears to occurs between these western plants and those found in the mountains of northeastern Pakistan, northern India, and Nepal. The two allopatric portions of the range of *S. virgaurea* are separated by very dry areas of mountains and lowlands in Afghanistan, Turkmenistan, Uzbekistan, and western and central Kazakhstan. A polygenomic study comparing large numbers of samples of *S. virgaurea* and *S. dahurica* is needed to clarify the geographic limits of the two species. Such a study could also show whether or not high alpine forms of the *S. virgaurea* are derived multiple times from closely related lower elevation populations or if all of the high alpine forms across Europe are of a single origin. In short, is *S. minuta* L. a real taxon or a polyphyletic assemblage of regional dwarf alpine ecotypes? Such a molecular study is also likely to reveal whether *S. virgaurea* is native to the Himalaya Mountains or if the plants with hairs over much or all of the fruit body surface are in fact extremely hairy forms of *S. dahurica*. Individuals treated a priori as *S. dahurica*, *S. decurrens*, and *S. virgaurea* in the analysis of just those species were placed a posteriori into those species with significant probability for a high majority of the specimens, but the analysis heavily weighted the total numbers of ovary/fruit body hairs. Two specimens from Pakistan

and two from Xinjiang Prov., China were included in the *S. dahurica* a priori group. One specimen each from Pakistan and Xinjiang were placed with very high probability into *S. dahurica*, while the other specimens were placed with high probability into *S. virgaurea* among the cluster of specimens that included the specimen from Kyrgyzstan (Fig. 37). Of the 5 specimens of *S. virgaurea* assigned to other species, all were from Europe and had sparsely hairy ovary/cypsela bodies and were assigned a posteriori to either *S. dahurica* or *S. decurrens*, although it is highly unlikely that specimens from Austria, Estonia, and Switzerland belong to those two Asian species.

The names *Solidago virgaurea* subsp. *leiocarpa* and *S. virgaurea* var. *leiocarpa* have been misapplied in the literature for many decades (e.g. Iwatsuki 1985; Sakaguchi et al. 2018). The basionym *Amphirhapis leiocarpa* was proposed in 1842 based on *Hinds s.n.* (K!) collected in Hong Kong (see Table 1). There is only one species of *Solidago* native to southern China, *S. decurrens,* which was based on an unknown collection from Canton. No type collections appear to exist, but a neotype *Hinds s.n.* (K!) is designated in Table 1. The choice of neotype was logical because it is a historically significant collection and comes from the same provenance as the original material on which the name *S. decurrens* was based. The choice of neotype for *S. decurrens* also results in *Amphiraphis leiocarpa* and names based on the basionym being relegated to complete synonymy under the older name *S. decurrens*. Iwatsuki (1995) stated that var. *leiocarpa* was native to the southern Kuril Islands, Hokkaido, Sakhalin, Kamchatka and E. Siberia, but no taxon in *Solidago* as treated here has a range that includes all those locations (see Fig. 29). *Solidago dahurica* is native to E. Siberia, Kamchatka, and Sakhalin, but not northern Japan or the Kuril Islands. *Solidago pacifica* is native to the provinces and oblasts along the lower Amur River in China and Russia and "Manchuria" China, North Korea, and a few locations on northern Hokkaido Island, Japan. The names *S. virgaurea* subsp. *leiocarpa* and *S. virgaurea* var. *leiocarpa* cannot be legitimately applied to plants native to E. Siberia, Kamchatka, and Sakhalin. Such plants are either *S. dahurica*, *S. kurilensis*, or *S. pacifica*. *Solidago decurrens* does not occur in the southern Kuril Islands, Hokkaido, Sakhalin, Kamchatka, and E. Siberia. Sakaguchi et al. (2018) applied the name *leiocarpa* to a set of plants native to higher elevations on Hokkaido and Honshu. Sakagucki (pers. comm.) indicated that these are somewhat genetically differentiated from *S. decurrens* and *S. kurilensis* (synonym *S. nipponica*) and may be the result of possible hybridization and introgression of *S. decurrens* and *S. kurilensis* at higher elevations where the ranges of the two parent species are locally sympatric. Regardless of exactly what these plants are (a mixture of hybrids or ecotypes?), the name *leiocarpa* is not correctly applied to them.

The status of *Solidago pacifica* is problematic in terms of species limits. In the two multispecies analyses that included *S. pacifica* specimens, a posteriori placement into *S. pacifica* was only 56% in both analyses; nearly half the specimens assigned a priori to *S. pacifica* were placed into either *S. dahurica* or *S. decurrens*. The range of distribution of *S. pacifica* connects the allopatric ranges of *S. dahurica* and *S. decurrens* in northeastern China and North Korea where the ranges of all three are potentially sympatric. A large sample of plants from throughout North Korea is needed to increase the sample size of *S. pacifica*, but obtaining such collections seems unlikely at this time. Molecular data might reveal that *S. pacifica* is in fact an assemblage of robust *S. decurrens* and *S. dahurica* specimens that are atypical forms in marginal populations. Further work on *S. pacifica* is needed. In Table 1, the type of *S. virga-aurea* var. *gigantea* Nakai from Hokkaido is listed as a synonym of *S. pacifica*. Sakaguchi et al. (2018) did not include specimens under the name *S. pacifica*, although some of the Korean peninsula collections they sampled may belong in that species. It is also possible that some the northern Hokkaido collections labeled under the misapplied Bentham epithet *leiocarpa* or all of their Hokkaido samples belong in *S. kurilensis* (including *S. nipponica*).

It seems highly likely that all the native Eurasia taxa in *Solidago* are derived from a single North American branch of the genus and *S. macrophylla* is the only species native to North America

that is part of that branch today (J.B. Beck, pers. comm.). It also seems highly likely that *Solidago* migrated into Eurasia via Beringia at some time in the past during glacial times. Interestingly, only diploids are known in ser. *Solidago* and ser. *Macrophyllae*. *Solidago multiradiata* is the only native North American species that also is native to extreme eastern Eurasia (Chukotka Autonomous Okrug, Russia; a tetraploid count has been reported from Chukotka by Zhukova and Tikhonova 1971), but *S. multiradiata* is not closely related to the Eurasian ser. *Solidago*. Assuming the ancestor of ser. *Solidago* migrated via the same route and ultimately diverged into the species recognized here in the same way and for the same reasons that the genus has diverged into more than 100 species relatively quickly in North America, the more distant a Eurasia population of *Solidago* is from extreme northeastern Russia the more divergent it is from the original ancestor of ser. *Solidago*. Traditionally, *S. virgaurea* has been defined very broadly to include nearly all taxa in the genus native to Eurasian in multiple subspecies and varieties. The only exceptions recognized as separate species in Iwatsuki et al. (1995) were *S. minutissima* and *S. yokusaiana*, but these are native to southern Japan and are adapted to well defined habitats and are morphologically distinct from *S. decurrens* (synonym: *S. virgaurea* var. *asiatica*). It is not logically consistent to include most of the Eurasian *Solidago* taxa in *S. virgaurea* but to separate these two taxa as species. *Solidago horieana* was not described in 1995, but might also might also have been treated as a distinct species by Iwatsuki et al. (1995) because it too is confined to a specific habitat on Hokkaido Island. The highly informative results of Sakaguchi et al. (2018) indicate that there is a north to south divergence of genomes within Japan with divergence into special habitats in Hokkaido (*S. horieana*), central and southern Honshu (*S. yokusaiana*), the Izu archipelago (*S. decurrens* var. *praeflorens*) and the Ryukyu Arc (*S. minutissima* on Yaku-shima and S. *decurrens* var. *insularis* further south). Sample sizes in this multivariate study for var. *praeflorens* and var. *insularis* were too small to reach final conclusions about whether or not they differ sufficiently from *S. decurrens* to warrant species rank, although the differences among the three varieties of *S. decurrens* are not large in our opinion. It might be logically more consistent to also treat *S. minutissima* as a variety within *S. decurrens*, but the results of the multivariate study indicate that species status is not unwarranted. The results of Sakaguchi et al. (2018) are basically in agreement with the results of this multivariate study, although their nomenclatural choices obscure this similarity in findings. Our conclusion is that the same kind of divergence in molecular traits will be found following ser. *Solidago* from east to west across Eurasia as Sakaguchi et al. (2018) found following the series from north to South in Japan. Expanding the molecular sample to include plants from southern China, Vietnam, and the northern Phillipines and eastern India could reveal whether or not *S. decurrens* diverged in a similar fashion and whether all three of these possible migration routes are examples of repeated founder effect reduction in overall genome diversity, with *S. dahurica* being the most diverse genetically in ser. *Solidago* and the most phylogenetically basal taxon in the series. Do the Kamchatka populations represent persistent early members of ser. *Solidago* or are they also the result of divergence via founder effect from a possible glacial peak refugium for the entire series somewhere further south on mainland eastern Asia? Multivariate methods are not suited to resolving these questions.

Key to taxa in *Solidago* ser. *Solidago*

1. Cypselae very sparsely to densely strigulose over the entire ovary/fruit body; Europe, Morocco, Turkey, and the Himalaya mountains of India and Nepal
    2. Lower stems and leaves glabrous to only very sparsely strigose; Europe, Morocco, Turkey, and Himalaya mountains of India and Nepal ..... **Solidago virgaurea**
    2. Vegetative portions of plants densely strigose to villose-strigose; sand dune habitats along coast between the mouths of Magra (Liguria) and Cecina (Tuscany) rivers, Italy ..... **Solidago litoralis**
1. Cypselae glabrous or sparsely to moderately strigulose only distally (some *S. dahurica* individuals can be more hairy on the upper lower half of the fruit body).

2. Inflorescences usually somewhat corymbiform; blade of lower leaves truncate; Kuril Islands, Hokkaido, northern Honsho, Japan ..... **Solidago kurilensis**
2. Inflorescccences narrowly to broadly paniculiform; blade of lower leaves tapering; most of temperature zone Asia

3. Stem 2-15 cm tall; higher elevations, Yaku-shima, Japan ..... **Solidago minutissima**
3. Stems 20-100 cm tall; most of temperature zone Asia

4. Stem leaves narrow, gradually reduced upward, sometimes somewhat triple-nerved; rheophyte on rocks along rivers in southern Japan ..... **Solidago yokusaiana**
4. Stem leaves much reduced upward, leaves never triple-nerved; various habitats in Asia

5. Involucres (5-)**7-8**-10 mm tall
6. Cypselae usually only sparsely hairy distally; central Asia to northern China and Kamchatka ..... **Solidago dahurica**
6. Cypselae densely strigose; rheophyte on rocks in streams of serpentine areas of northern Hokkaido, Japan ..... **Solidago horieana**

5. Involucres 3.5-**5.6**-7 mm tall; various habitats in eastern Asia and eastern India

7. Phyllaries somewhat obtuse; plants robust; greater lower Amur R. drainage China and southeastern Russia, North Korea, "Manchuria" China ..... **Solidago pacifica**
7. Phyllaries lanceolate, acute; stems short to rarely 1+ m tall but leaves much reduced upward; eastern India, central, eastern and southern China, northern Viet Nam, higher elevations on Luzon Is., Philippines, Taiwan, Japan ..... **Solidago decurrens**
8. Flowering January to May; mid stem leaves crowded on mid stems, lower above ground stems persisting for years; Ryukyu Is., Japan ..... **S. d. var. insularis**
8. Stems blooming in summer and fall; mid stem leaves not crowded; stems dormant in winter
9. Cypselae strigose distally; Izu archepeligo, Japan .....**S. d. var. praeflorens**
9. Cypselae glabrous; South Korea, eastern China south into northern Vietnam and Luzon Is., Phillipines, eastern India, Taiwan and Japan .....**S. d. var. decurrens**

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NEW RECORDS OF ARACEAE FOR COSTA RICA AND PANAMA

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ABSTRACT

Four species are documented for the first time for the Costa Rican flora: *Anthurium curvispadix*, *Anthurium palosecense*, *Monstera integrifolia*, *Monstera spruceana.* Two species are first documented for the Panamanian flora: *Monstera costaricensis* and *Monstera epipremnoide*s.

The Cordillera de Talamanca is a biodiverse mountain range shared between Costa Rica and Panama and includes one of the most important protected areas in Central America, La Amistad International Park (Hammel et al. 2004; Monro et al. 2017). It contains a series of suitable habitats for the Araceae family (Croat 2019, pers. comm.).

The Araceae are widely distributed in Costa Rica and Panama at elevations ranging from 0 to 2800 m, showing high diversity mainly at middle elevations and lowland rainforests (Grayum 2003). In the Talamanca mountain range, the Araceae are represented mainly by the genera *Anthurium*, *Monstera*, *Philodendron*, and *Stenospermation*. Additionally, it is considered the center of diversity for the genus *Monstera* (Cedeño-Fonseca et al. 2018; Madison 1977; Zuluaga & Cameron 2018) and it is a region of high endemism for *Anthurium* and *Philodendron*, especially the Panamanian part (Croat 2019, pers. comm.).

Despite several expeditions to the Talamanca mountain range by the National Museum of Costa Rica (CR), the Missouri Botanical Garden (MO), and the Natural History Museum of London (BM), the appearance of new records is frequent (Monro et al. 2017). During recent herbarium studies and fieldwork documenting the Araceae family in parts of Costa Rica and Panama (including the Talamanca mountain range), species of the genus *Anthurium* and *Monstera* were collected that

constitute new distribution records. The collected samples were compared with the material housed at the Herbarium of the National Museum of Costa Rica (CR), Missouri Botanical Garden (MO) and the Herbarium of the University of Panama (PMA).

NEW RECORDS FOR COSTA RICA

1. ANTHURIUM CURVISPADIX Croat, Ann. Missouri Bot. Gard. 78: 639. 1991.

TYPE: **PANAMA**. **Colón**. Santa Rita Ridge Road, along trail at end of road which goes to Río Indio, beginning 10.6 km from Transisthmian Hwy, 3 km beyond hydrographic station, 09°22'30"N, 079°41'30"W, 380 m, 13 Apr 1976, *T.B. Croat 34294* (holotype: MO!; isotypes: K, MO!, PMA!, SEL, US).

New records. COSTA RICA. **Puntarenas**. Buenos Aires, P.N. La Amistad, Cuenca Térraba-Sierpe, fila que va desde el albergue Rancho Amuo a Cerro Seno, bosque denso de 5–25 m, predominado por *Cedrela tonduzii*, *Sloanea ampla*, *Quercus*, *Magnolia sororum*, sotobosque con Geonoma sp., 09°07'12"N, 083°05'18"W, 1800–1900 m, 25 Feb 2008, *Santamaria 7209* (CR, PMA).

Distribution. Costa Rica and Panama at 20–1900 m.

Comments. *Anthurium curvispadix* is a member of sect. *Calomystrium*, characterized by having broadly ovate to ovate-triangular leaf blades, long, marcescent cataphylls that do not disintegrate, pale whitish-green recurved spathes, and tapered and curved creamy white spadices. In Costa Rica, this species could be confused with *A. hoffmannii* Schott, which differs in having shorter cataphylls (up to 15 cm long), a parabolic to spathulate sinus, and shorter and less tapered or straight spadices (<9.0 cm long vs. >9.0 cm long).

2. ANTHURIUM PALOSECENSE Croat & O. Ortiz, Aroideana 39: 175. 2016.

TYPE: **PANAMA**. **Bocas del Toro**. Bosque Protector Palo Seco, área boscosa a los alrededores de Williemazu, 09°9'29"N, 082°30'29"W, 363 m, 1 Feb 2013, *O. Ortíz 1202* (holotype: MO!; isotype: PMA!).

New records. COSTA RICA. **Limón**. Z.P. Rio Banano, cuenca del Rio Banano, Valle de La Estrella, Fila Matama, ca. 11 km SW del pueblo de Aguas Zarcas, camino que lleva al rancho El Hotel, bosque nuboso primario, 09°49'27"N, 083°09'42"W, 700–800 m, 19 Oct 2007, *Santamaria 6496* (CR, PMA).

Distribution. Costa Rica and Panama at 200–800 m.

Comments. *Anthurium palosecense* is similar to *A. talamancae* Engl. (sect. *Polyneurium*), but differs in having leaf blades usually markedly cordate, subcordate to sagittate at base (vs. rounded to subcordate in *A. palosecense*), with 3–5 pairs of basal veins (vs. 1–2 basal veins) and longer (8–17 cm vs. up to 4.8 cm long) and wider (4–8 mm vs. 2–3 mm diam.) dark maroon to dark violet purple spadices (vs. yellowish to orange-red spadices).

3. MONSTERA INTEGRIFOLIA Zuluaga & Croat, Phytotaxa 334: 6, f. 4A–C, 5A–E. 2018.

TYPE: **PANAMA**. **Chiriqui**. Distrito Gualaca, corregimiento Hornito, Reserva Forestal Fortuna, trails near to research center Jorge L. Arauz. 1200–1500 m, 82°12.8'N, 8°47'W, 31 Jan 2013, *A. Zuluaga 916* (holotype: WIS; isotypes: MO, PMA).

New records. COSTA RICA. **Cartago**. Turrialba, Chirripó, Moravia de Chirripó, bosque nuboso, 9°46'2''N 83°25'21.6''W, 1602 m, 20 Dec 2019 (fr.), *Cedeño, Karremans, Chinchilla, Rojas 1638* (USJ); Turrialba, Chirripó, Moravia de Chirripó, bosque nuboso, 9°46'2''N 83°25'21.6''W, 1602 m, 20 Dec 2018 (fr.), *Cedeño, Karremans, Chinchilla, Rojas 1639* (USJ [2 parts]); Turrialba, Chirripó, Tayutic, Jicotea, Siguiendo la Fila Vereh, entre la Cueva del Sapo y Fila Vereh, 9°45'0''N

83°33’0’’W, 1634 m, 22 Dec 2018 (fl., fr.), *Herrera 8005* (CR, MO [2 dupl.]). **Heredia**. Sarapiqui, La Virgen, primary forest along Rio San Rafael, Atlantic slope of Volcan Barva, 10°13’0’’N 84°5’0’’W, 1500 m, 12 Apr 2019 (fr.), *Grayum 7017* (MO). Figure 1.

Distribution. Costa Rica and Panama at 1000–1700 m.

Comments. *Monstera integrifolia* is recognized by having narrow leaf blades with primary lateral veins that arise from the midrib at an angle of 35°, whitish and mottled petioles, with a petiolar sheath that disintegrates as fibrous residues, and flowers with a conical stigmatophore. It could be confused with *M. anomala* Zuluaga & Croat and *M. standleyana* G. Bunting, but *M. standleyana* plants are usually more robust, have a columnar stigmatophore, and inhabit at lower elevations (0–1360 m). On the other hand, *M. anomala* never has fenestrated leaf blades and the flowers have an elongated style with a constriction in the middle. *Monstera integrifolia* was described by Zuluaga & Cameron (2017) as a new species for Costa Rica and Panama. However, the paratype cited for Costa Rica (*Croat 66170*, MO) is actually *M. epipremnoides* Engl.

4. MONSTERA SPRUCEANA (Schott) Engl., Fl. Bras. 3(2): 115. 1878. *Tornelia spruceana* Schott, Oesterr. Bot. Z. 9(2): 40. 1859.

TYPE: **BRAZIL**. [**Amazonas**]. Rio Negro, São Gabriel, *R. Spruce 2293* (holotype: K!; photos: BH, BR, GH, NY, S).

New records. COSTA RICA. **Alajuela**. Upala, slope of Cerro Cacao, E to near Río Las Haciendas, 10°57’0’’N 85°27’0’’W, 1150 m, 14 Aug 2007 (sterile), *Grayum 12713* (MO). **Puntarenas**. Puntarenas, Monteverde, camino a Tilarán, 10°21’58.6’’N 84°51’12.6’’W, 1325 m, 21 Nov 2018 (fr.), *Cedeño & Cascante 1501* (USJ [2 parts]); Osa, Bahía Drake, camino a Rancho Quemado, 8°40’51.1’’N 83°33’32.6’’W, 188 m, 3 Feb 2019 (sterile), *Cedeño & Hay 1621* (USJ); Osa, Sierpe, along road between Rincon and Boscosa, 2 km W of bridge over Rio Rincon, 8°41’20’’N -83°29’50’’W, 50 m, 11 Sep 1996 (fr), *Croat 79253* (CR, MO [2 parts]). Figure 2.

Distribution. Costa Rica to Bolivia, Brazil, Venezuela and the Guayanas at 50–1600 m.

Comments. *Monstera spruceana* is recognized by its pinnatilobate adult leaf blade, the slightly verrucose or smooth petiole, sheathed up to the base of the geniculum or even up to the base of the blade, the petiolar sheath disintegrating as fibrous residues, short peduncles (<10 cm), long spadices (15–25 cm), and dark green stylar caps after the anthesis. It is similar to *M. anomala,* but this latter species is distinguished by its completely entire leaves, by the constricted stylar region, and by its occurrence (at least in Costa Rica and Panama) in lowland humid forests.

Both the description of *Monstera spruceana* by Grayum (2003), including the specimen cited there, as well as the other Costa Rican samples previously identified under this name correspond to the recently described *M. anomala* (Zuluaga & Cameron 2017). However, the samples listed below were identified as *M. spruceana* during this study.

In Costa Rica, *Monstera spruceana* has been collected only in cloud forests at 1200–1600 m and in lowlands in the Osa Peninsula (50 m). However, it has not been found at intermediate elevations, and only the populations in the Osa Peninsula and the Tilarán mountain range are known. Populations in Panama also grow in lowland humid forests and in cloud forests at 1200 m. In Colombia, it grows both in lowlands (Choco and Amazon regions) and cloud forests (parts of the Andean Western Cordillera). The populations in Panama and Colombia have some differences with those of Costa Rica; therefore, this species requires more study in the field to document the morphology of the flowers and the developing spathe in anthesis.

NEW RECORDS FOR PANAMA

1. MONSTERA COSTARICENSIS (Engl. & K. Krause) Croat & Grayum, Ann. Missouri Bot. Gard. 74: 659. 1987. *Rhodospatha costaricensis* Engl. & K. Krause in Engl., Pflanzenr. IV.23B (Heft 37): 95. 1908.

TYPE: **COSTA RICA**. [**Limón**.] Ferme de Boston, Atlantic watershed, 30 m elev., [10°01' N, 83°15'30"W], *A. Tonduz 14628* (holotype: B!).

New records. PANAMA. Bocas del Toro, 08°46'43"N 082°12'32"W, 1047 m, 25 Aug 2018 (fr.), *Ortiz et al. 3367* (MO, PMA). Figure 3.

Distribution. Costa Rica, Nicaragua and Panama at 0–1047 m.

Comments. *Monstera costaricensis* is recognized by the stem and verrucose petiole with white dots, persistent and markedly undulated petiolar wings (a unique feature in the genus), the leaf blade with an entire margin and few fenestrations, the perforations that develop mainly near the midrib, and the primary lateral veins parallel. Adult individuals are robust and become fertile when they grow on trees with diameters greater than 45 cm.

2. MONSTERA EPIPREMNOIDES Engl., Bot. Jahrb. Syst. 37: 118. 1905.

SYNTYPES: **COSTA RICA**. [**San José**]. Santa María de Dota, 1300 m, 4 Apr 1890, *H. Pittier 2486* (lectotype, designated by Madison [1977: 63]: B! [photos: BH, SEL, as *P. Biolley 2846*]; isolectotypes: CR! as *P. Biolley 2846*, BR! as *H. Pittier 2486*). **COSTA RICA**. [**San José**.] La Uruca, 1100 m, Jul 1890, *P. Biolley 2846* (CR in part; specimens in B and BR with this number are in fact *Pittier 2486*). See Madison (1977).

New records. **PANAMA**. Chiriquí, 08°50'N 082°43'W, 1200-1400 m, 11 Jul 1983 (fr.), *Hamilton & Krager* 3766 (MO). Figure 4.

Distribution. Costa Rica and Panama at 1200–2200 m.

Comments. *Monstera epipremnoides* is recognized by having mottled or white petioles, persistent sheaths with open wings, pinnatifid blades with fenestrations adjacent to the midrib, the externally yellowish green spathe which is up to 13 cm longer than the spadix, and the circular stigmas, slightly raised by stigmatophores. *Monstera epipremnoides* grows in the pre-montane forests of the Talamanca mountain range.

ACKNOWLEDGEMENTS

Marco Cedeño-Fonseca thanks the Organization for Tropical Studies for a Glaxo-Wellcome research grant and the Rexford Daubenmire Fellowship, which supported fieldwork for the project "Taxonomy of the genus *Monstera* (Alismatales: Araceae) for Costa Rica," an Alwyn H. Gentry Fellowship from the Missouri Botanical Garden, and a Mini-ARTS Fellowship from the Society of Systematic Biologists, which allowed him to study herbarium material at the Missouri Botanical Garden, the Marie Selby Botanical Gardens, and the New York Botanical Garden. Michael Mittermeier, Cristina Goettsch Mittermeier, and Caroline Sparks also helped in raising funds for travel through a Gofundme.com campaign. We are grateful to the Ministerio de Ambiente y Energía de Costa Rica (MINAE) and its Sistema Nacional de Áreas de Conservación (SINAC) for issuing the scientific permits under which wild specimens were collected. This contribution represents part of the Master's thesis of Marco Cedeño-Fonseca, completed in the Programa de Posgrado en Biología at Universidad de Costa Rica.

Figure 1. *Monstera integrifolia*. (A) Adult plant. (B) Juvenile plant. (C) Whitish petioles, with somewhat persistent sheaths (arrow). (D) Left: developing infructescence with short, conical styles. Right: whitish petiole with green sheath speckled with white dots (arrow). Photographs: M. Cedeño-Fonseca.

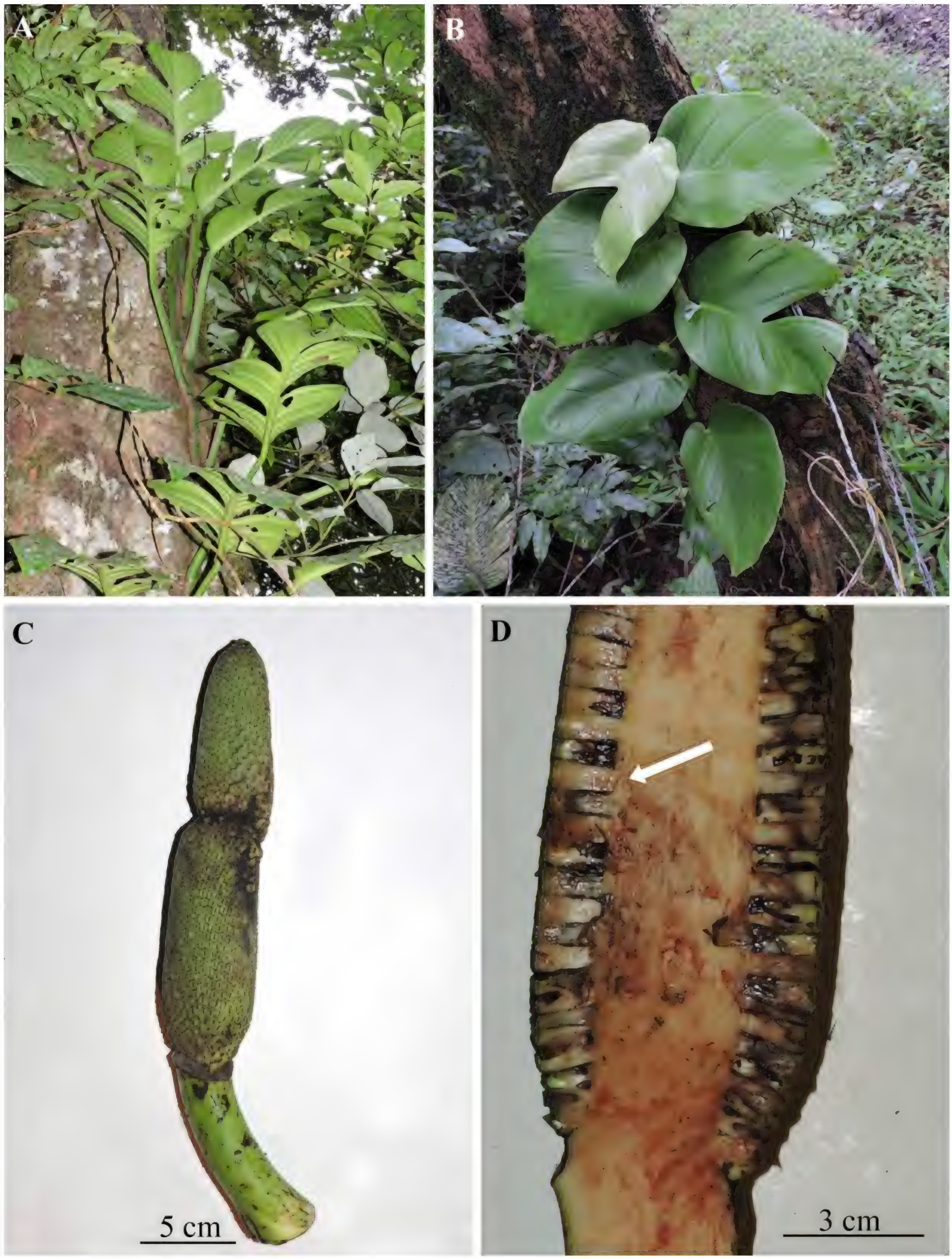

Figure 2. *Monstera spruceana*. (A) Adult plant. (B) Juvenile plant. (C) Developing infructescence. (D) Longitudinal section of the spadix to show the shape of the ovary (arrow). Photographs: M. Cedeño-Fonseca.

Figure 3. *Monstera costaricensis*. (A) Adult individual. (B) Markedly undulate petiole sheath reaching to the base of the leaf blade. (C) Developing infructescence with warty peduncle and persistent cataphyll (arrow). (D) Infructescence with pyramidal and conical styles. Photographs: M. Cedeño-Fonseca.

Figure 4. *Monstera epipremnoides*. (A) Adult individual. (B) Petioles speckled with white and green dots. Photographs: M. Cedeño-Fonseca.

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Nesom, G.L. 2020. *Erythranthe plotocalyx* (Phrymaceae), a new species from Arizona and New Mexico. Phytoneuron 2020-40: 1–9. Published 15 July 2020. ISSN 2153 733X

ERYTHRANTHE PLOTOCALYX (PHRYMACEAE), A NEW SPECIES FROM ARIZONA AND NEW MEXICO

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ABSTRACT

Plants from southern Arizona and southwestern New Mexico are described as **Erythranthe plotocalyx** Nesom, **sp. nov.**, of sect. *Mimulosma*. They have been identified as *E. floribunda*, which occurs in the same area, but are distinct in their combination of erect habit (not procumbent and rooting at nodes), epetiolate leaves, long, ascending-erect peduncles, inflated calyces, and cleistogamous flowers with small corollas.

A revision of *Erythranthe* sect. *Mimulosma* (Nesom 2012) documented populations in southern Arizona and southwestern New Mexico that are distinct from apparently closely related *E. floribunda* but which appeared to intergrade. Continued examination *E. floribunda* over its wide range in the USA and Mexico has emphasized the morphological distinction of these variants and their restricted geography, and it is not clear that apparent intermediates actually represent gene flow involving *E. floribunda*. Previous tentative identifications of these collections and populations as *M. floribundus*, *M.* "probably *floribundus*," *M. latidens*, *M. primuloides*, *M. pulsiferae*, and *M. rubellus* further emphasize their distinction and they are formally described here at specific rank.

Erythranthe plotocalyx Nesom, **sp. nov.** **TYPE**: **New Mexico**. Hidalgo Co.: Peloncillo Mts., Clanton Draw, 3.0 mi E of the [Coronado] National Forest, E side property line, 5480 ft, annual in mud at edge of stream, 9 May 2004, *R.D. Worthington 32511* (holotype: ASU; isotypes: NMC, SRSC, UNM, UTEP). Figures 3, 4, and 5.

Similar to *Erythranthe floribunda* (sect. *Mimulosma*) in its annual duration, glandular vestiture, and small flowers but distinct in the combination of erect habit (not procumbent and rooting at nodes), more elongate and sessile to subsessile (epetiolate) leaves with attenuate bases and palmately 3–5-nerved venation, long, ascending-erect pedicels, inflated calyces, and flowers with small corollas.

Annual, fibrous-rooted. **Stems** (3–)6–30 cm, erect to ascending-erect. **Stems, pedicels,** and **calyces** villous-glandular with gland-tipped hairs. **Leaves** cauline, basal mostly deciduous by flowering, oblanceolate to elliptic or elliptic-lanceolate, basally attenuate to sessile or subsessile, epetiolate, 11–27 mm x 3–10 mm, primarily palmately 3–5-nerved, sometimes with an additional 1–2 smaller lateral pairs, margins entire to shallowly serrate or dentate with 1–3 pairs of teeth. **Fruiting pedicels** 20–45 mm long. **Fruiting calyces** distinctly inflated, suburceolate, 5–8 mm long, greenish or purplish, not red-dotted, villous-glandular, lobes subequal, triangular-acuminate. **Corollas** yellow with floor of tube red-dotted, exserted 2–4 mm beyond the calyx, tube-throats funnelform-cylindric, 5–6 mm long, limbs essentially radially symmetric, expanded 3–4 mm across (pressed), lobes broadly oblong-obovate, apically notched. **Style** and **stigma** exserted 1–2 mm beyond calyx margin. Figures 1-9.

Flowering April–July. Around grassland cienegas and seasonal drainages, wet meadows, along sandy washes, wet soil in marshes, pond and creek edges; 3000–5500 ft.

Additional collections examined. **Arizona**. Cochise Co.: Riggs Settlement, ca. 45 km (by air) ESE of Wilcox, Sulphur Springs Valley, 31° 00.387' N, 109° 26.396' W, desert grassland, small cienega formed along Pine Creek from gravel extraction, 4960 ft, 18 Jun 2019, *Roll RS0023* (ARIZ). Coconino Co.: Williams, wet meadow, 6 Jul 1889, *Greene s.n.* (NDG-2 sheets). Pima Co.: S end of Baboquivari Mts., in

sand along edge of Presumido Wash near Buenos Aires, ca. 3000 ft, 3 Apr 1966, *Mason 2559* (ARIZ). Santa Cruz Co.: Meadow Hills Country Club, 4.5 mi N of Nogales, wet soil in marsh, [ca. 3900 ft], 5 May 1966, *Crutchfield 1460* (LL); Santa Rita Mts., 4500 ft, 17 Apr 1903, *Thornber 505* (UC). **New Mexico**. Hidalgo Co.: 30 mi S of Animas, edges of ponds near and sandy banks of Animas Creek, 5000 ft, 19 Jun 1973, *Todsen s.n.* (NMC).

1. Plants erect to ascending-erect; cauline leaves basally attenuate to sessile or subsessile, epetiolate, blades oblanceolate to elliptic or elliptic-lanceolate, primarily palmately 3–5-nerved, sometimes with an additional 1–2 smaller lateral pairs; fruiting pedicels 20–45 mm; corolla tube-throats 5–6 mm; fruiting calyces 5–8 mm long ..... **Erythranthe plotocalyx**
1. Plants laxly erect to decumbent, sprawing, or procument; cauline leaves abruptly and distinctly petiolate, blades generally ovate with a rounded to truncate or cordate base; mostly pinnately to subpalmately veined; fruiting pedicels 5–15(–26) mm; corolla tube-throats (4–)5–10 mm, fruiting calyces 4–7 mm long ..... **Erythranthe floribunda**

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Figure 1. *Erythranthe plotocalyx*. Santa Cruz Co., Arizona, west edge of Grosvenor Hills. Photo by Sue Carnahan, 2 April 2019, documenting *Carnahan 3656* (ARIZ).

Figure 2. *Erythranthe plotocalyx.* Santa Cruz Co., Arizona. Photo by Sue Carnahan, as in Fig. 1.

Figure 3. *Erythranthe plotocalyx.* Hidalgo Co., New Mexico One of several plants from *Worthington 32511* (SRSC isotype).

Nesom: *Erythranthe plotocalyx*, sp. nov.

Figure 4. *Erythranthe plotocalyx.* Hidalgo Co., New Mexico. *Worthington 32511* (ASU, holotype).

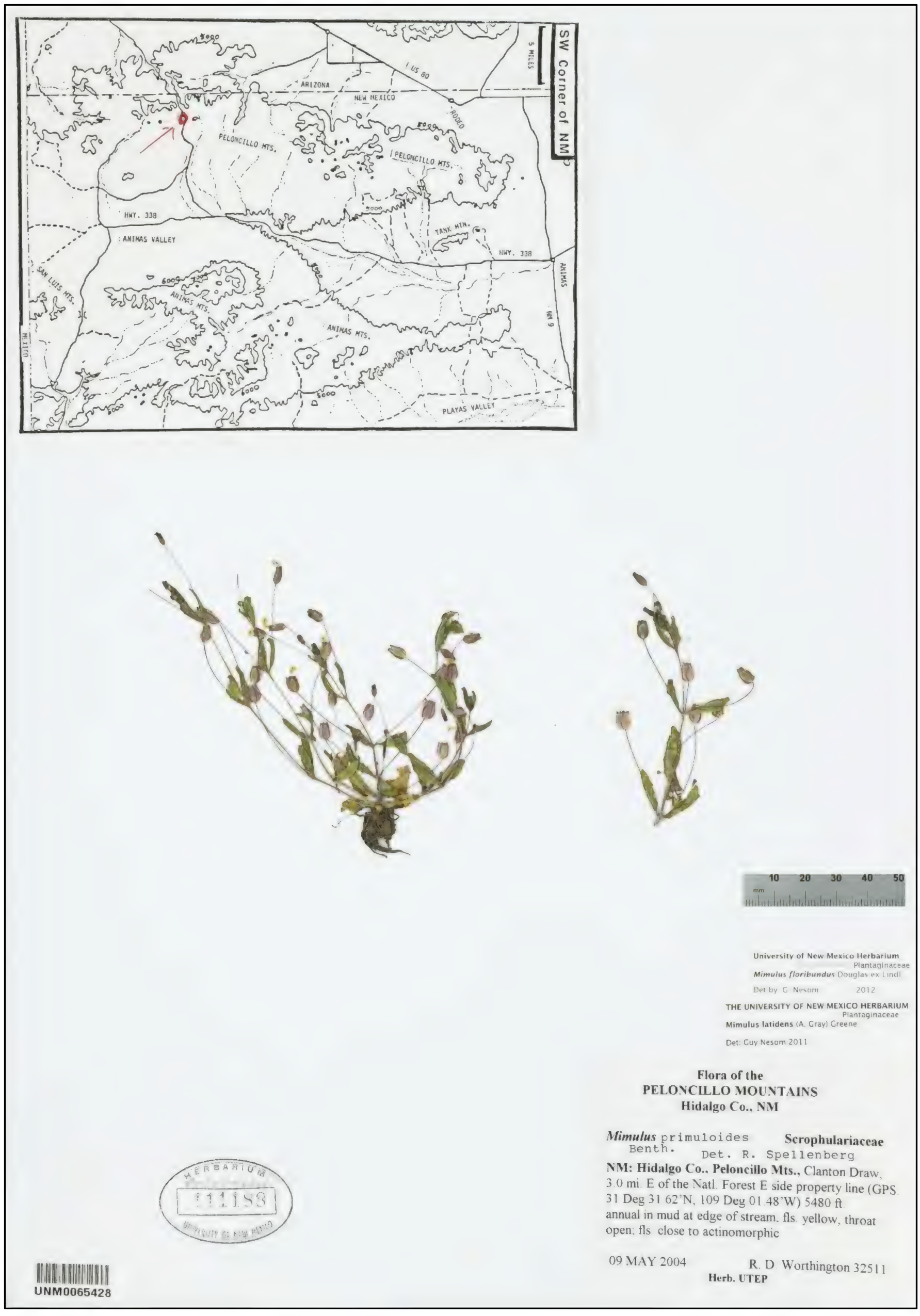

Figure 5. *Erythranthe plotocalyx*. Hidalgo Co., New Mexico. *Worthington 32511* (UNM, isotype).

Figure 6. *Erythranthe plotocalyx.* Hidalgo Co., New Mexico. *Todsen s.n.* (NMC).

Figure 7. *Erythranthe plotocalyx.* Cochise Co., Arizona. *Roll RS0023* (ARIZ).

Figure 8. *Erythranthe plotocalyx.* Coconino Co., Arizona. *Greene s.n.* ND-G).

Figure 9. *Erythranthe plotocalyx.* Coconino Co., Arizona. *Greene s.n.* (ND-G).

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ERIOBOTRYA JAPONICA (ROSACEAE) NEW FOR THE ARKANSAS FLORA

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ABSTRACT

Eriobotrya japonica (Thunb.) Lindl. is reported here for the first occurrence in Arkansas outside of cultivation. These plants were at the edge of a highly disturbed greenbelt in the city of Arkadelphia, Clark Co., in close proximity to a large cultivated plant of *E. japonica* at the greenbelt edge. Spontaneous *Eryiobotrya* seedlings also occur at other sites in Clark County in the vicinity of cultivated plants. Photographs of spontaneous *E. japonica* plants in habitat are provided.

Spontaneous plants of *Eriobotrya japonica* (Thunb.) Lindl. (loquat) were discovered in 2014 at the edge of a disturbed, urban greenbelt in Clark County, Arkansas (Fig. 1). These plants were juveniles (all less than 2 meters tall) established from a large, presumably cultivated plant of *E. japonica* at the greenbelt edge. Large numbers of spontaneous individuals of the species also have been observed at other Clark County sites (Figs. 2–4).

Voucher specimen. **Arkansas.** Clark Co.: Arkadelphia, W of intersection of University Dr. and N 8th St., numerous spontaneous juvenile plants at edge of expansive urban greenbelt, with a large, cultivated plant of *E. japonica* in the immediate vicinity, 13 Nov 2014, *Serviss 8145* (HEND).

Figure 1. A–B. *Eriobotrya japonica* escaped in Clark Co., Arkansas. Several escaped plants, two of which are shown here, were at the edge of an urban greenbelt in Clark Co., Arkansas.

Eriobotrya japonica is a small, evergreen tree to 10 meters that is native to China (Bailey & Bailey 1976; Krüssmann 1977; Gu & Spongberg 2003—Fig. 5). It is cultivated in the southern USA and throughout southeastern Asia for its juicy, sweet fruit and fragrant flowers (Gu & Spongberg 2003; Phipps 2014). *Eriobotrya japonica* has been documented in the USA from a number of other southern states, including Louisiana and Texas (Thomas & Allen 1998; Hrusa et al. 2002; Judd 2003; Carter et al. 2009; Payne 2010; Wunderlin & Hansen 2011; Phipps 2014; Kartesz 2015; USDA, NRCS 2020). This genus and species previously have not been documented from Arkansas outside of cultivation (Arkansas Vascular Flora Committee 2006; Gentry et al. 2013).

Figure 2. A–D. Spontaneous, juvenile *Eriobotrya japonica* plants in Clark Co., Arkansas. These plants are from a different location than those shown in Figure 1. Plants were repeatedly established at this site over multiple years by seeds from cultivated ones. A–B. Plants in 2009; several individuals may be seen in both photographs. C. Plant in 2006. D. Plant in 2010.

The presence of spontaneous plants of *Eriobotrya japonica* in Arkansas is not surprising, and should be expected in areas where plants of the species are cultivated (and elsewhere) in the southern portion of the state. Based on our observations, *E. japonica* appears to have high potential to become established in the state's flora.

In Arkansas, the large (up to 30 centimeters long), coriaceous, coarsely toothed leaves clearly distinguish *Eriobotrya japonica* from most other woody species. It potentially could be confused with *Photina serratifolia* (Chinese photina) or *Magnolia grandiflora* (southern magnolia); however, it easily may be distinguished from both species by the dense indument of grayish-brown to rusty-brown, tomentose trichomes on young stems, twigs, lower leaf surfaces, and inflorescences. Additionally, the leaves of *M. grandiflora* have entire margins.

Figure 3. Evidence of prolific seeding by *Eriobotrya japonica* in Clark Co., Arkansas. Over 10 spontaneous plants may be seen in the photograph; more plants were present at the site than what is shown.

Figure 4. Slightly older spontaneous plants of *Eriobotrya japonica* in Clark Co., Arkansas. Seven plants may be seen in the photograph. The plants in Figures 3 and 4 were seeded from cultivated plants.

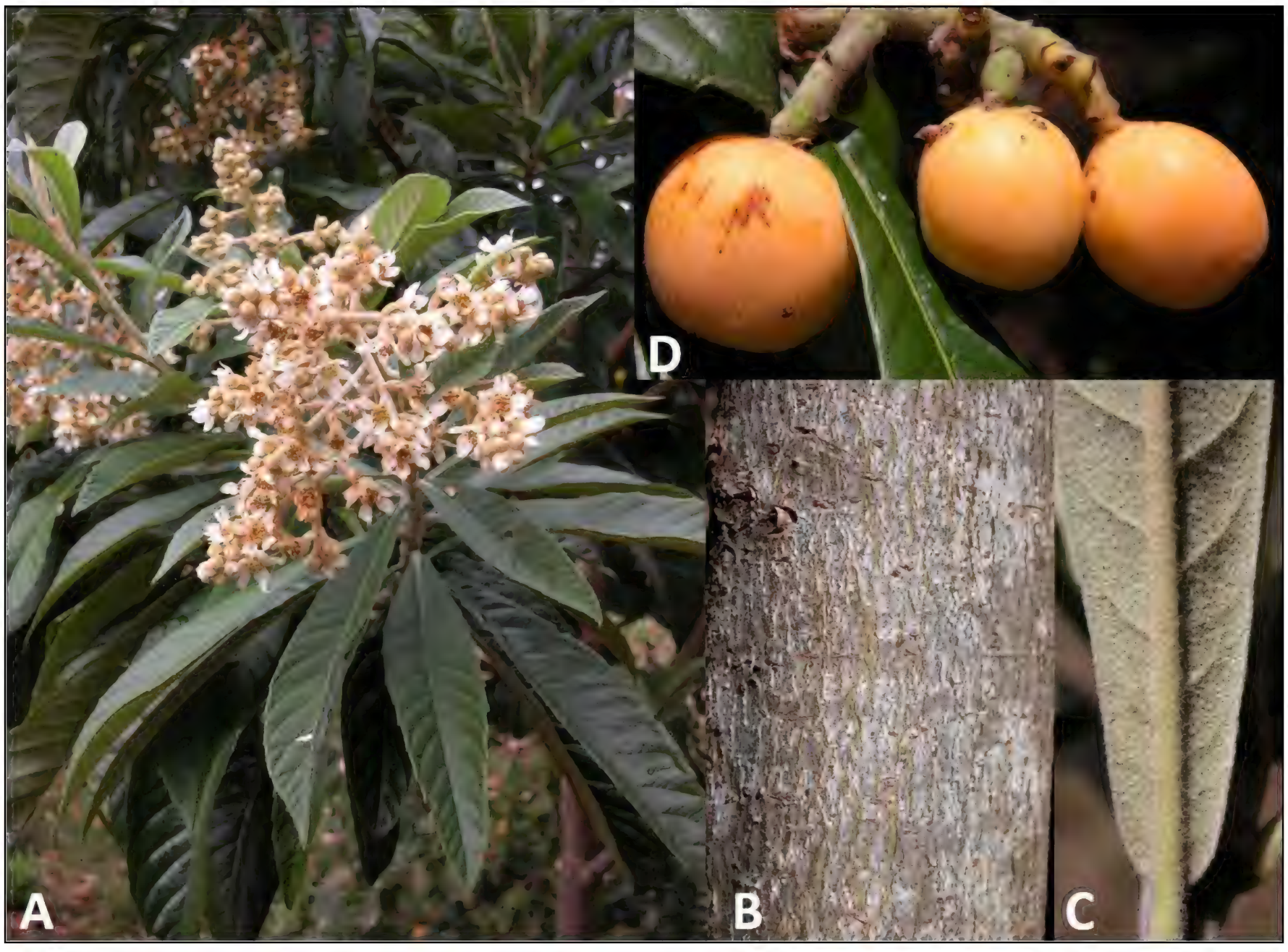

Figure 5. A–D. *Eriobotrya japonica* plant and habit. A. Leaves and inflorescences. B. Bark. C. Lower surface of leaf showing indument of tomentose trichomes. D. Mature fruits.

ACKNOWLEDGEMENTS

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CORRECTIONS TO PHYTONEURON 2019-77: VALIDATIONS OF NAMES OF NEW TAXA

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The names of four new taxa of Montiaceae appearing in Phytoneuron in Hershkovitz (2019a; see also Hershkovitz, 2019b) were not validly published per Art. 40.6 (see also Art. 9, Note 6) of the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al. 2018). Three of the names are validated here and the fourth is replaced by a name of a new taxon at a different rank.

CISTANTHE SUBSPECIOSA Hershk., **sp. nov.** **TYPE**: **CHILE**. Atacama Region. Tierra Amarilla Province. Tierra Amarilla, ca. 700 m elev., Sep 1924, *Werdermann 405* (holotype: E image! <http://data.rbge.org.uk/herb/E00033178>; isotypes: F!, U! image! <http://data.biodiversitydata.nl/naturalis/specimen/U.1523945>, US!).

Diagnosis. Plants pertaining phylogenetically to *Cistanthe* sect. *Cistanthe*, morphologically similar to but distinct from (1) *Cistanthe cabrerae* (Añon) Peralta and *Cistanthe grandiflora* (Lindl.) Schltdl. [incl. *C. cachinalensis* (Phil.) Peralta & D.I. Ford and probably *Calandrinia taltalensis* I.M. Johnst.] in having normally 80–100 rather than ca. 50 stamens in fully developed flowers and a long (ca. 15 mm) exserted rather than shorter (< 10 mm) style; and from (2) *Cistanthe laxiflora* (Phil.) Peralta & D. I. Ford in having a herbaceous to suffruticose rather than fruticose habit, broadly ovate rather than narrowly obovate to lanceolate and more succulent leaves, and leafy inflorescence stems.

Hershkovitz (2019c) provided a more detailed discussion of this species.

CISTANTHE sect. **THYRSOIDEAE** Hershk., **sect. nov.** **TYPE** (designated here): *Cistanthe thyrsoidea* (Reiche) Peralta & D.I. Ford. Synonym: *Calandrinia thyrsoidea* Reiche, Fl. Chile 2: 342. 1898 and Anales Univ. Chile, I, Mem. Ci. Lit. 100: 342. 1898.

Diagnosis. Plants similar to other species of *Cistanthe* but differing in having, in the range of rDNA-ITS1 base positions 70–80, a five-base motif, "C]TCCCT[C" instead of a three-base motif, "C]-CTC-[C."

This section includes the species referred in Hershkovitz (2019a) to "*Cistanthe* sect. *Rosulatae* subsect. *Thyrsoideae*" (nom. inval., Art. 40.6).

THINGIA Hershk., **gen. nov.** **TYPE**: *Thingia ambigua* (S. Wats.) Hershk.

Thingia ambigua (S. Wats.) Hershk., **comb. nov.** *Claytonia ambigua* S. Wats., Proc. Amer. Acad. Arts 17: 365. 1882. *Calandrinia ambigua* (S. Wats.) Howell, Erythea 1: 34. 1893. *Cistanthe ambigua* (S. Wats.) Carolin ex Hershk., Phytologia 68: 269. 1990. **TYPE**: *J.G. Lemmon 117* (holotype: GH image!).

Diagnosis. Montiaceae-Cistantheae-Calyptridinae: differing from *Calyptridium* Nutt. and *Philippiamra* Kuntze in having two rather than three carpels; differing from *Lenzia* Phil. in having leafy stems and branched inflorescences rather than being acaulescent with solitary and axillary flowers; and differing from all three of these genera in having three-dimensional basket-like leaf venation rather than two-dimensional (planar) venation.

ACKNOWLEDGEMENTS

I thank John McNeill (E) for revision and comments.

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BERGIA TEXANA (ELATINACEAE) AND *ELEOCHARIS ATROPURPUREA* (CYPERACEAE): FIRST RECORDS FOR ARIZONA

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ABSTRACT

Recent collections of *Bergia texana* and *Eleocharis atropurpurea* from desert grassland around the Pat Hills of Cochise Co., Arizona, are documented and illustrated. While both species are known from surrounding states and Mexico, these collections represent the first verified occurrences for these species in Arizona.

In an ongoing floristic inventory of the Pat Hills desert grassland of Cochise County (Roll 2018, 2020), two additions to the known flora of Arizona have been documented. *Bergia texana* (Elatinaceae) and *Eleocharis atropurpurea* (Cyperaceae) were collected from the moist soil around a stock pond located at the base of one of the largest hills. This stock pond catches runoff readily and holds the water for extended periods of time. The discovery of these taxa in Arizona was not unexpected, however, since their presence in nearby states and Mexico has been previously documented (Kearney & Peebles 1973; Lehr 1978; PLANTS Database 2020; SEINet 2020). Records for these taxa are presented below.

Bergia texana (Hook.) Seub. ex Walp.

USA. **Arizona**. Cochise Co.: Pat Hills, ca. 30 km (20 mi) by air SE of Willcox, Sulphur Springs Valley, 32° 00.061' N 109° 35.384' W, elev. 1389 meters (4558 feet), uncommon herbaceous annual in dried mud of an empty stock pond in alluvium at base of andesitic hillside, 8 Dec 2015, *Roll 1660* (ARIZ); locally common herbaceous annual in wet soil around same stock pond, 30 Sep 2016, *Roll 2371* (ARIZ, ASU, DUR) and 14 Oct 2016, *Roll 2418* (DES, NMC).

Native to North America and known from California, New Mexico, Texas, Sonora, and other states in both the USA and Mexico. Figure 1.

Eleocharis atropurpurea (Retz.) J. & K. Presl.

USA. **Arizona**. Cochise Co.: Pat Hills, ca. 30 km (20 mi) by air SE of Willcox, Sulphur Springs Valley, 32° 00.061' N 109° 35.384' W, elev. 1389 meters (4558 feet), locally common herbaceous annual in wet soil around stock pond in alluvium at base of andesitic hillside, 18 Sep 2016, *Roll 2361* (ASC, ARIZ, ASU, DES) and 30 Sep 2016, *Roll 2376* (ARIZ, DUR).

Native to North America and known from California, New Mexico, Texas, Sonora, and other states in both the USA and Mexico. Figure 2.

Figure 1. *Bergia texana*. Photo by author, 30 Sep 2016.

Figure 1. *Eleocharis atropurpurea*. Photo by author, 18 Sep 2016.

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Tom Van Devender and Ana Lilia Reina-Guerrero have given invaluable assistance with the Pat Hills flora project and with preparation of this note. For their generous assistance with identifications, I thank Max Licher (*Eleocharis*) and Socorro González-Elizondo (*Bergia*).

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VASCULAR PLANTS OF THE PAT HILLS DESERT GRASSLAND, SOUTHEAST ARIZONA

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ABSTRACT

A checklist is provided for the vascular plant flora of the Pat Hills desert grassland located south of Willcox in the Sulphur Springs Valley of Cochise County in southeastern Arizona. A total of 480 taxa of vascular plants in 288 genera and 73 families have been recorded in the study area since March of 2015. *Erigeron decrescens* was documented as a species new to science from the Pat Hills. *Bergia texana* and *Eleocharis atropurpurea* have been reported as additions to the Arizona flora. Also, a new population of *Pediomelum pentaphyllum*, a plant of conservation concern, was located.

The grasslands of the Sulphur Springs Valley of Cochise County in southeastern Arizona represent an example of the extensive North American desert grassland that approaches its northern limit in Arizona, New Mexico, and Texas. Most of this desert grassland extends to the southeast into central Mexico (McClaran & Van Devender 1995). The study area includes the Pat Hills and adjacent grasslands, which are located in the Sulphur Springs Valley between the Willcox Playa to the west and the Chiricahua mountains to the east (Fig. 1). Within the study area are over 15,000 acres (6,000 hectares) of land, most of which is privately owned, that has been used for grazing cattle for at least the past 100 years (Riggs & Roll 1951).

Elevations range from approximately 1,275 to 1,525 meters (4,400 to 5,000 feet). Precipitation generally ranges from approximately 20 to 30 centimeters (8 to 12 inches) per year (James Riggs, Willcox, Arizona, pers,. comm., 7 March 2018; PRISM Climate Group, 24 Mar 2018). Southeastern Arizona has a bi-seasonal rainfall pattern with both winter and summer wet periods. The summer rains (May through October) account for approximately 60–70% of the annual rainfall (Martin 1963). Plants respond with two distinct growth and flowering periods, spring (March to May) and summer monsoon (mid-July to October) (Crimmins et al. 2008).

Current vegetation is desert grassland interspersed with a complement of shrubs and forbs, and with halophytic scrub in alkaline areas. There are no active springs, but a number of stock ponds hold water for various periods of the year. There is also the remnant of what is known locally as the Pat Burns Ciénega. This ciénega flowed intermittently at the end of the 19th century, but today it is an occasionally wet alkaline floodplain lying immediately to the south of the Pat Hills (Meinzer & Kelton 1913). Ephemeral watercourses from the Chiricahua Mountains both to the north and south of the Pat Hills historically flowed west into the Willcox Playa, and prehistorically into ancient Lake Cochise (Meinzer & Kelton 1913).

Both the Pat Hills and the Pat Burns Cienega are named after Pat Bierne, whose last name was sometimes spelled as Burn. In 1878 Mr. Bierne (Burn) located a cattle ranch at the ciénega that now bears his name (Barnes 1935).

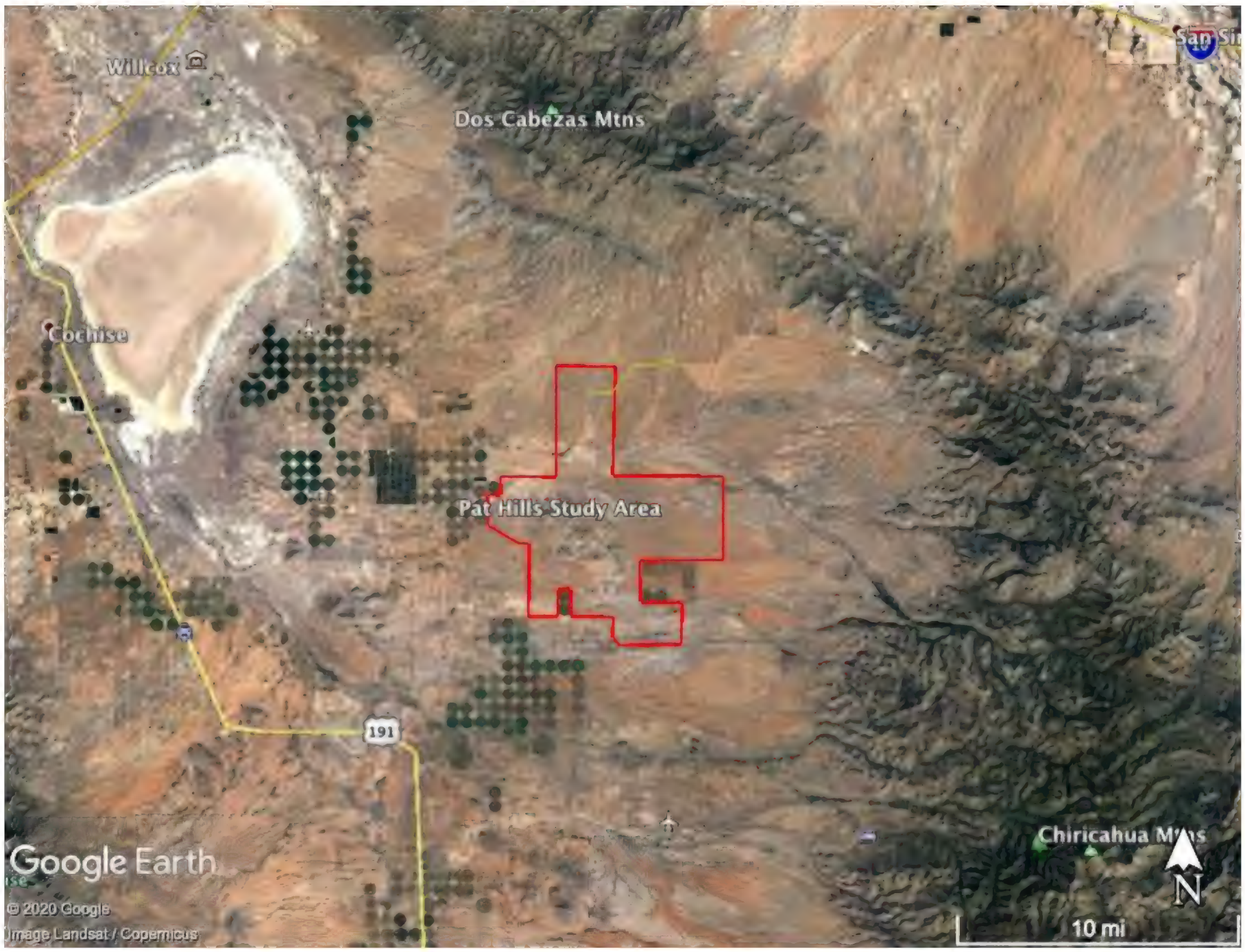

Figure 1. Pat Hills Desert Grassland Study Area, Cochise Co., Arizona.

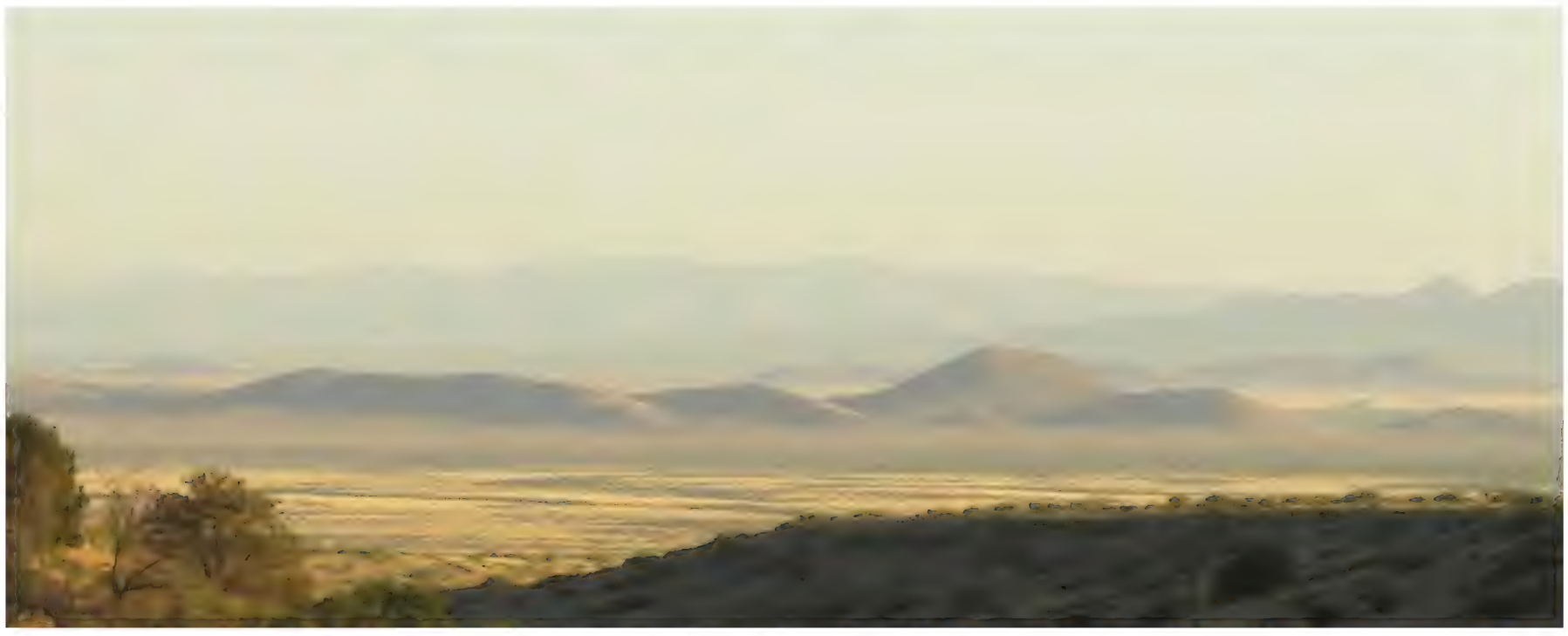
Figure 2. Pat Hills as seen from Dos Cabezas Mts., looking south. Photo by Michael Witt.

The rocks that make up the Pat Hills were formed by one volcano that was active during two distinct periods of time around the end of the Cretaceous Period (around 65 million years ago). The extrusions of volcanic material apparently occurred in a non-explosive manner. Massive deposits of porphyritic andesite, porphyritic dacite, and quartz diorite-granodiorite (represented in early geologic maps as granite) are common, along with later deposits of rhyolite, quartz monzonite, and other materials. Although the volcano may have once been over 1,600 meters (5,200 feet) high, erosion has

reduced it to the existing range of small hills (Ettinger 1962). There is no exposed limestone within the study area, but there are areas with large amounts of "caliche," a calcareous evaporite deposit, in the soil (Meinzer & Kelton 1913). The hills are surrounded by deep alluvial fans.

Very few plant collections from the Pat Hills have been found in regional herbaria. This may be due to the private ownership of the land or its relative distance and inaccessibility from established highways. In 1884 Marcus E. Jones made early botanical collections in the nearby areas of Willcox, Dos Cabezas, and Bowie. John J. Thornber made substantial collections from 1905 through 1916 around the communities of Cochise, Willcox, and Light (now non-existent) and from the Dos Cabezas Mountains. Lyle A. McGill made collections in the area from 1970 through 1984. Elizabeth Makings published the Flora of the San Pedro Riparian National Conservation Area in 2006 (Makings 2006). That flora includes a desert grassland component that is similar to that of the Pat Hills area.

This floristic inventory of the Pat Hills and adjacent grassland began in March 2015 and will continue into the future. Preliminary results were presented at the Madrean Conference 2018, held in Tucson (Roll 2018). More complete inventory results are presented here as a list of vascular plants. A total of 480 taxa of vascular plants in 288 genera and 73 families have been recorded by observation or collection. Approximately 6% of the taxa are introduced, with most being grasses. Approximately 13% of the taxa are subshrubs, shrubs, or trees, including a number of trees and shrubs that occur only in the ephemeral watercourses flowing from the Chiricahua Mountains or as introductions around an abandoned residence and stock ponds.

During this inventory, a new species was discovered and has been described (Nesom & Roll 2020). *Erigeron decrescens* Nesom & Roll was first discovered in an occasionally wet depression in a small draw east of the Pat Hills in the spring of 2019 and it subsequently has been found in extensive drainages with *Hilaria mutica*, and at the margins of wet areas outside of the study area. It is a winter annual, germinating with the late fall and winter rains and flowering from late March and into May. This new species grows in association with the annual *Erigeron divergens* and the perennial *Erigeron incomptus*.

Of other taxa recorded in the checklist, two are additions to the known flora of Arizona. *Bergia texana* (Elatinaceae) and *Eleocharis atropurpurea* (Cyperaceae) were collected from the moist soil around a stock pond located at the base of one of the largest hills. This particular stock pond catches runoff readily and holds the water for extended periods of time. The discovery of these taxa in Arizona was not unexpected, since their presence in nearby states and Mexico has been previously documented (Roll 2020).

In addition, a new population of the rare *Pediomelum pentaphyllum* (Fabaceae) was located. A petition to list this plant under the U. S. Endangered Species Act was filed in 2008 (Wild Earth Guardians 2008). That petition is currently under investigation and consideration by the U.S. Fish and Wildlife Service. Other populations of this plant are located in southwestern New Mexico and in southeastern Arizona. Populations of *Leuciva dealbata* (Asteraceae) were discovered in the Pat Hills area and appear to represent a western extension of range of this plant.

More than 160 days were spent collecting in the field during 2015, 2016, 2017, 2018, and 2019. Extensive use has been made of the Southwestern Environmental Information Network (SEINet) database for the purposes of plant identification, label production, and flora preparation in this study. Herbarium vouchers or photographic documentation for all taxa listed below have been made. Observations and collections have been entered into the SEINet database and vouchers have been deposited in the University of Arizona Herbarium, with duplicates in other local herbaria. Full collection or observation data for all specimens are available in SEINet.

Plant taxa are listed alphabetically by family, genus, and species. In some cases, determination to subspecies or variety is shown. Following the name is the author's collection number in parenthesis, representing in most cases a voucher specimen at the University of Arizona Herbarium (ARIZ). Where plant material was not collected and only photographic vouchers were made, the word 'SEINet' is included within the parenthesis. Those photographic vouchers have been entered into SEINet.

The Pat Hills lie at the western edge of an extensive open grassland landscape covering more than 100,000 acres, bounded by the Dos Cabezas Mountains to the north and the Chiricahua Mountains to the east. Efforts are currently underway by the Trust for Public Land, New Mexico Land Conservancy, Arizona Game and Fish Department, Arizona Land and Water Trust, and other agencies to protect this unique landscape and its integral biological diversity. The area is at risk from the encroachment of irrigated agriculture and other forms of potential development. Through the use of conservation easements and other conservation tools, efforts are under way to maintain the integrity of this uninterrupted swath of desert grassland. It is hoped that the present study will provide useful basic information to assist in that important work.

VASCULAR PLANTS OF THE PAT HILLS DESERT GRASSLAND

ACANTHACEAE
Anisacanthus thurberi (Torr.) A. Gray (2879)
Carlowrightia arizonica A. Gray (170)

AIZOACEAE
Trianthema portulacastrum L. (715)

AMARANTHACEAE
**Alternanthera caracasana* Kunth (904)
Amaranthus blitoides S. Wats. (2521)
Amaranthus palmeri S. Wats. (821)
Atriplex canescens (Pursh) Nutt. (175)
Atriplex elegans (Moq.) D. Dietr. (753)
Atriplex wrightii S. Watson (749)
Chenopodium berlandieri Moq. (1435)
Chenopodium desiccatum A. Nels. (853)
Chenopodium fremontii S. Watson (852)
Chenopodium incanum (S. Watson) Heller (387)
Chenopodium incanum var. elatum Crawford (412)
Chenopodium leptophyllum (Moq.) Nutt. ex S. Wats. (1245)
Chenopodium neomexicanum Standl. (470)
Chenopodium watsonii A. Nels. (1055)
Froelichia arizonica Thornb. ex Standl. (695)
Gomphrena caespitosa Torr. (225)
Gomphrena nitida Rothrock (762)
Guilleminea densa (Humb. & Bonpl. ex Willd.) Moq. (415)
**Kochia scoparia* (L.) Schrad. (2274)
Krascheninnikovia lanata (Pursh) A.D.J. Meeuse & Smit (461)
Monolepis nuttalliana (J.A. Schultes) Greene (1768)
Salsola tragus L. (380)
Tidestromia lanuginosa (Nutt.) Standl. (921)

AMARYLLIDACEAE
Allium kunthii G. Don (769)
Zephyranthes longifolia Hemsl., also *Habranthus longifolius* (Hemsl.) Flagg, G. Lom. Sm. & Meerow (439)

APIACEAE
Cymopterus multinervatus (Coult. & Rose) Tidestrom (1)
Daucus pusillus Michx. (307)
Eryngium heterophyllum Engelm. (1399)
Lomatium nevadense var. *parishii* (Coult. & Rose) Jepson (2847)
Lomatium orientale Coult. & Rose (1863)
Spermolepis lateriflora G.L. Nesom (47)

APOCYNACEAE
Asclepias asperula (Dcne.) Woods. (456)
Asclepias brachystephana Engelm. ex Torr. (247)
Asclepias nummularia Torr. (1963)
cf. *Asclepias nyctaginifolia* A. Gray (2820)
Asclepias subverticillata (A. Gray) Vail (394)
Asclepias uncialis Greene (1860)
Funastrum crispum (Benth.) Schltr. (251)
Funastrum hartwegii (Vail) Schltr. (401)
Mandevilla brachysiphon (Torr.) Pichon (588)

ARACEAE
Lemna minor L. (1036)

ARISTOLOCHIACEAE
Aristolochia watsonii Woot. & Standl. (139)

ASPARAGACEAE
Agave palmeri Engelm. (810)
Agave parryi var. *huachucensis* (Baker) Little ex L. Benson (284)
Dasylirion wheeleri S. Wats. (270)
Dichelostemma capitatum (Benth.) Wood (42)
Echeandia flavescens (J.A. & J.H. Schultes) Cruden (633)
Yucca elata (Engelm.) Engelm. (335)

ASTERACEAE
Acourtia nana (A. Gray) Reveal & King (146)
Acourtia wrightii (A. Gray) Reveal & King (158)
Almutaster pauciflorus (Nutt.) A.& D. Löve (1251)
Ambrosia confertiflora Dc. (657)
Ambrosia monogyra (Torr. & A. Gray) Strother & B.G. Baldwin (1066)
Artemisia dracunculus L. (2257)
Artemisia ludoviciana Nutt. (839)
Baccharis pteronioides DC. (109)
Baccharis salicifolia (Ruiz & Pav.) Pers. (1591)
Baccharis sarothroides A. Gray (1185)
Baccharis wrightii A. Gray (1257, 1962)
Bahia absinthifolia Benth. (73)
Baileya multiradiata Harvey & A. Gray ex A. Gray (129)
Berlandiera lyrata Benth. (928)
Bidens leptocephala Sherff (746)
Brickellia californica (Torr. & A. Gray) A. Gray (1148)
Brickellia coulteri A. Gray (540)
Brickellia eupatorioides (L.) Shinners (1174)
Brickellia floribunda A. Gray (1615)
Brickellia venosa (Woot. & Standl.) B.L. Robins. (371)
Calycoseris wrightii A. Gray (224)
Chaenactis stevioides Hook. & Arn. (55)
Chaetopappa ericoides (Torr.) G.L. Nesom (77)
Cirsium neomexicanum A. Gray (242)
Cirsium ochrocentrum A. Gray (352)
Dietaria verna (Raf.) Morefield (2932)
Dyssodia papposa (Vent.) A.S. Hitchc. (1247)
Ericameria laricifolia (A. Gray) Shinners (1547)
Ericameria nauseosa (Pallas ex Pursh) G.L. Nesom & Baird (1635)
Erigeron arisolius G.L. Nesom (446)
Erigeron canadensis L., also *Conyza canadensis* (L.) Cronq. (880)
Erigeron decrescens Nesom & Roll (2865)
Erigeron divergens Torr. & A. Gray (2866, 2886)
Erigeron incomptus A. Gray (2885)
Erigeron tracyi Greene (1293)
Flourensia cernua DC. (1612)
Gaillardia pulchella Foug. (65)
Gamochaeta stagnalis (I.M.Johnst.) Anderb. (2856)
Grindelia nuda var. *aphanactis* (Rydb.) G.L. Nesom (911)
Gutierrezia sarothrae (Pursh) Britt. & Rusby (389)
Hedosyne ambrosiifolia (Gray) Strother (567)
Helianthus laciniatus A. Gray (2814)
Helianthus petiolaris Nutt. (282)
Heliomeris longifolia (Robins. & Greenm.) Cockerell (1212)
Heterotheca psammophila B. Wagenkn.

(872)
Hymenothrix wislizeni A. Gray (507)
Isocoma tenuisecta Greene (688)
**Lactuca serriola* L. (301)
Laennecia coulteri (A. Gray) G.L. Nesom (464, 731)
Laennecia sophiifolia (Kunth) G.L. Nesom (619)
Leuciva dealbata (Gray) Rydb. (2594)
Logfia filaginoides (Hook. & Arn.) Morefield (2857)
Machaeranthera tagetina Greene (847)
Machaeranthera tanacetifolia (Kunth) Nees (385)
Malacothrix fendleri A. Gray (117)
Parthenium incanum Kunth (494)
Pectis filipes Harvey & A. Gray (659)
Pectis papposa Harvey & A. Gray (2343)
Pectis prostrata Cav. (919)
Pseudognaphalium canescens (DC.) Anderb. (1026)
Pseudognaphalium leucocephalum (A. Gray) A. Anderb. (873)
Pseudognaphalium stramineum (Kunth) W.A. Weber (1025)
Psilactis brevilingulata Schultz-Bip. ex Hemsl. (407)
Psilactis gentryi (Standl.) D. Morgan (1391)
Ratibida columnifera (Nutt.) Woot. & Standl. (452)
Sanvitalia abertii A. Gray (767)
Schkuhria pinnata (Lam.) Kuntze ex Thell. (2818)
Senecio flaccidus Less. (273)
**Sonchus asper* (L.) Hill (198)
Stephanomeria exigua Nutt. (228.1)
Stephanomeria pauciflora (Torr.) A. Nels. (741)
Stephanomeria tenuifolia (Raf.) Hall (1982)
Stylocline sonorensis Wiggins (2854)
Thelesperma megapotamicum (Spreng.) Kuntze (641)
Thymophylla acerosa (DC.) Strother (1923)
Thymophylla pentachaeta var. *belenidium* (DC.) Strother (1913)
Thymophylla pentachaeta var. *pentachaeta* (DC.) Small (184)
Trixis californica Kellogg (236)
Uropappus lindleyi (DC.) Nutt. (1835)
Verbesina encelioides (Cav.) Benth. & Hook. f. ex A. Gray (211)
Viguiera cordifolia A. Gray (1002)
Xanthisma gracile (Nutt.) D.R. Morgan & R.L. Hartm. (791)
Xanthisma spinulosum (Pursh) D.R. Morgan & R.L. Hartman (2861)
Xanthium strumarium L. (850)
Zinnia acerosa (DC.) A. Gray (118)
Zinnia grandiflora Nutt. (157)

BIGNONIACEAE
Chilopsis linearis (Cav.) Sweet (2101)

BIXACEAE
Amoreuxia palmatifida Moc. & Sessé ex DC. (476)

BORAGINACEAE
Amsinckia tessellata A. Gray (2870)
Cryptantha crassisepala (Torr. & A. Gray) Greene (50)
Cryptantha micrantha (Torr.) I.M. Johnston, also *Eremocarya micrantha* (Torr.) Greene (303)
Cryptantha nevadensis A. Nels. & Kennedy (314)
Cryptantha pterocarya var. *cycloptera* (Greene) J.F. Macbr. (130)
Eucrypta micrantha (Torr.) Heller (2582)
Lappula occidentalis var. *cupulata* (A. Gray) Higgins (84)
Lappula occidentalis var. *occidentalis* (S. Wats.) Greene (2588)
Nama hispidum A. Gray (40)
Pectocarya platycarpa (Munz & Johnston) Munz & Johnston (29)
Pectocarya recurvata I.M. Johnston (2576)
Phacelia arizonica A. Gray (43)
Phacelia crenulata Torr. ex S. Wats. (131)
Plagiobothrys arizonicus (A. Gray) Greene ex A. Gray (1794)

BRASSICACEAE
Descurainia pinnata (Walt.) Britt. (18)

**Descurainia sophia* (L.) Webb ex Prantl (1726)
Draba cuneifolia Nutt. ex Torr. & A. Gray, also *Tomostima cuneifolia* (Nutt. ex Torr. & A. Gray) Al-Shebbaz, M. Koch & Jordan-Thaden (2843)
Hesperidanthus linearifolius (A. Gray) Rydb. (522)
Lepidium lasiocarpum Nutt. (13)
Lepidium oblongum Small (1805)
Lepidium thurberi Woot. (24)
Lepidium virginicum L. (1868)
Physaria gordonii (A. Gray) O'Kane & Al-Shehbaz (5)
Planodes virginicum (L.) Greene (1804)
**Sisymbrium irio* L. (16)
Thysanocarpus curvipes Hook. (2832)

CACTACEAE
Coryphantha vivipara (Nutt.) Britt. & Rose (206 SEINet)
Cylindropuntia leptocaulis (DC.) Knuth (1572)
Cylindropuntia leptocaulis x C. spinosior (858)
Cylindropuntia spinosior (Engelm.) Knuth (135 SEINet)
Echinocereus fendleri (Engelm.) Sencke ex J.N. Haage (82 SEINet)
Echinocereus rigidissimus (Engelm.) Haage *f.* (358 SEINet)
Ferocactus wislizeni (Engelm.) Britt. & Rose (653 SEINet)
Mammillaria heyderi Muehlenpfordt (1964 SEINet)
Mammillaria wrightii var. *wilcoxii* (Toumey ex K. Schum.) W.T. Marsh. (652 SEINet)
Opuntia engelmannii Salm-Dyck (142 SEINet)
Opuntia macrocentra Engelm. (356)
Opuntia phaeacantha Engelm. (355)

CANNABACEAE
Celtis reticulata Torr. (246)

CARYOPHYLLACEAE
Loeflingia squarrosa Nutt. (2855)
Silene antirrhina L. (2841)

CLEOMACEAE
Polanisia dodecandra ssp. *trachysperma* (Torr. & A. Gray) Iltis (2801)

COMMELINACEAE
Commelina erecta L. (687)

CONVOLVULACEAE
Convolvulus equitans Benth. (345)
Evolvulus alsinoides (L.) L. (479)
Evolvulus arizonicus A. Gray (440)
Evolvulus nuttallianus Roem. & Schult. (143)
Evolvulus sericeus Sw. (136)
Ipomoea costellata Torr. (939)
Ipomoea cristulata Hallier f. (2332)
Ipomoea hederacea Jacq. (779)

CUCURBITACEAE
Apodanthera undulata A. Gray (475)
Cucurbita digitata A. Gray (871)
Cucurbita foetidissima Kunth (453)
Marah gilensis Greene (2303)

CYPERACEAE
Cyperus acuminatus Torr. & Hook. ex Torr. (1625, 2415)
**Cyperus difformis* L. (2375)
Cyperus esculentus L. (726)
Cyperus flavicomus Michx. (2307)
Cyperus sphaerolepis Boeckl. (595)
Cyperus squarrosus L. (1255)
Eleocharis atropurpurea (Retz.) J. Presl & C. Presl (2361, 2376)
Eleocharis macrostachya Britton (2864)
Eleocharis palustris (L.) Roemer & J.A. Schultes (558)
Eleocharis parishii Britt. (2878)
Fimbristylis annua (All.) Roemer & J.A. Schultes (2297)

ELATINACEAE
Bergia texana (Hook.) Seub. ex Walp. (1660, 2371)
Elatine rubella Rydb. (1583)

EPHEDRACEAE
Ephedra trifurca Torr. ex S. Wats. (21)

EUPHORBIACEAE
Acalypha neomexicana Müll. Arg. (2389)
Croton pottsii Klotzsch) Müll. Arg. (76)
Argythamnia neomexicana Müll. Arg. (154)
Euphorbia abramsiana L.C. Wheeler (2325)
Euphorbia albomarginata (Torr. & A. Gray) (111)
Euphorbia davidii Subils (709)
Euphorbia dioica Hieron. (2453)
Euphorbia exstipulata Engelm. (2345)
Euphorbia fendleri Torr. & A. Gray (147.1)
Euphorbia hyssopifolia L. (740)
Euphorbia micromera Boiss. ex Engelm. (2800)
Euphorbia serpyllifolia Pers. (699)
Euphorbia serrula Engelm. (2353)
Euphorbia stictospora Engelm. (755)
Tragia nepetifolia Cav. (2522)
Tragia ramosa Torr. (101)

FABACEAE
Acaciella angustissima (Mill.) Britton & Rose (159)
Acmispon brachycarpus (Benth.) D.D. Sokoloff (35)
Acmispon greenei (Wooton & Standl.) Brouillet (264)
Astragalus allochrous A. Gray (79)
Astragalus arizonicus A. Gray (72)
Astragalus mollissimus Torr. (8)
Astragalus nothoxys A. Gray (2639)
Astragalus nuttallianus DC. (31)
Astragalus thurberi A. Gray (329)
**Caesalpinia gilliesii* (Hook.) Wallich ex D. Dietr., also *Erythrostemon gilliesii* (Wall. ex Hook.) Klotzsch (229)
Calliandra eriophylla Benth. (133)
Calliandra humilis var. *reticulata* (A. Gray) L. Benson (2500)
Chamaecrista nictitans (L.) Moench (936)
Crotalaria pumila Ortega (879)
Dalea albiflora A. Gray (520)
Dalea brachystachya A. Gray (2516)
Dalea formosa Torr. (90)
Dalea jamesii (Torr.) Torr. & A. Gray (141)
Dalea lachnostachys A. Gray (2347)
Dalea nana var. *carnescens* Kearney & Peebles (92)
Dalea nana var. *nana* Torr. ex A. Gray (191)
Dalea pogonathera A. Gray (70)
Desmanthus cooleyi (Eat.) Trel. (372)
Desmodium neomexicanum A. Gray (952)
Galactia wrightii A. Gray (639)
Hoffmannseggia drepanocarpa A. Gray (551)
Hoffmannseggia glauca (Ortega) Eifert (83)
Lupinus concinnus J.G. Agardh (207)
Macroptilium gibbosifolium (Ortega) A. Delgado (585)
Marina calycosa (A. Gray) Barneby (120)
Mimosa biuncifera Benth. (179)
Pediomelum pentaphyllum (L.) J. Grimes (298, 318)
Phaseolus acutifolius var. *latifolius* Freeman (737)
Pomaria jamesii (Torr. & Gray) Walp. (188)
Prosopis glandulosa (Torr.) Cockerell (96)
Prosopis velutina Wooton (417)
Psoralidium tenuiflorum (Pursh) Rydb., also *Pediomelum tenuiflorum* (Pursh) A.N. Egan (2809)
Rhynchosia senna Gillies ex Hook. (148)
Senegalia greggii (A. Gray) Britton & Rose (2181)
Senna bauhinioides (A. Gray) Irwin & Barneby (234)
Sophora nuttalliana B.L. Turner (239)
Tephrosia tenella A. Gray (294, 316)
Vachellia constricta (Benth.) Seigler & Ebinger (361)

FAGACEAE
Quercus emoryi Torr. (1632)
Quercus turbinella Greene (531)

FOUQUIERIACEAE
Fouquieria splendens Engelm. (2563)

GERANIACEAE
**Erodium cicutarium* (L.) L'Hér. ex Ait. (10)
Erodium texanum A. Gray (2833)

JUNCACEAE
Juncus bufonius L. (2627)
Juncus interior Wiegand (2955)

KRAMERIACEAE
Krameria lanceolata Torr. (151)

LAMIACEAE
Clerodendrum coulteri (A. Gray) Govaerts (150)
Salvia subincisa Benth. (1248)

LINACEAE
Linum pratense (J.B.S. Norton) Small (2851)

LOASACEAE
Cevallia sinuata Lag. (128, 331)
Mentzelia albicaulis (Dougl.) Dougl. ex Torr. & A. Gray (1938)
Mentzelia montana (A. Davids.) A. Davids. (296)
Mentzelia multiflora (Nutt.) A. Gray (281)

LYTHRACEAE
Ammannia auriculata Willd. (2826)
Ammannia robusta Heer & Regel (2830)

MALPIGHIACEAE
Cottsia gracilis (A. Gray) W.R. Anderson (171, 486)

MALVACEAE
Abutilon abutiloides (Jacq.) Garcke ex Britt. & Wilson (535)
Abutilon mollicomum (Willd.) Sweet (650)
Abutilon parvulum A. Gray (160)
Anoda cristata (L.) Schlecht. (834)
Anoda pentaschista A. Gray (923)
Ayenia filiformis S. Wats. (181)
Hibiscus denudatus Benth. (127)
Malvella lepidota (A. Gray) Fryxell (138)
Rhynchosida physocalyx (A. Gray) Fryxell (419)
Sida abutifolia P. Mill. (132)
Sida spinosa L. (799)
Sphaeralcea angustifolia (Cav.) G. Don (85)
Sphaeralcea hastulata A. Gray (99)
Sphaeralcea laxa Woot. & Standl. (177)

MARSILEACEAE
Marsilea mollis B.L. Robins. & Fern. (293)

MARTYNIACEAE
Proboscidea althaeifolia (Benth.) Dcne. (450)
Proboscidea parviflora (Woot.) Woot. & Standl. (713)

MOLLUGINACEAE
Glinus radiatus (Ruiz & Pav.) Rohrb. (289)
**Mollugo cerviana* (L.) Ser. (2395)
Mollugo verticillata L. (697)

MONTIACEAE
Calandrinia ciliata (Ruiz & Pav.) DC. (33)
Cistanthe monandra (Nutt.) Hershkovitz (1871)
Phemeranthus aurantiacus (Engelm.) Kiger (534)

MORACEAE
Morus microphylla Buckl. (1139)

NYCTAGINACEAE
Allionia choisyi Standl. (2349)
Allionia incarnata var. villosa (Standl.) B.L. Turner (2824)
Boerhavia coccinea P. Mill. (732)
Boerhavia coulteri (Hook. f.) S. Wats. (590)
Boerhavia erecta L. (717)
Boerhavia pterocarpa S. Wats. (2247)
Boerhavia triquetra S. Wats. (2356)
Boerhavia wrightii A. Gray (1336)
Mirabilis linearis var. decipiens (Standl.) Welsh (2816)
Mirabilis linearis var. linearis (Pursh) Heimerl (503)

Mirabilis longiflora L. (2335)

OLEACEAE
Fraxinus velutina Torr. (1629)

ONAGRACEAE
Eremothera chamaenerioides (A. Gray) W.L. Wagner & Hoch (2599)
Gaura coccinea Nutt. Ex Pursh, also *Oenothera suffrutescens* (Ser.) W.L. Wagner & Hoch (97)
Gaura hexandra Ortega, also *Oenothera hexandra* (Ortega) W.L. Wagner & Hoch (68)
Oenothera albicaulis Pursh (46)
Oenothera flava (A. Nels.) Garrett (1773)
Oenothera primiveris A. Gray (30)

OROBANCHACEAE
Castilleja integra A. Gray (634)

PAPAVERACEAE
Argemone pleiacantha Greene (205)
Corydalis aurea Willd. (87)
Eschscholzia californica ssp. *mexicana* (Greene) C. Clark (39)

PHRYMACEAE
Erythranthe cordata (Greene) Nesom (2662)

PLANTAGINACEAE
Bacopa rotundifolia (Michx.) Wettst. (1580)
Nuttallanthus texanus (Scheele) D.A. Sutton (25)
Penstemon fendleri Torr. & A. Gray (276, 1862)
Plantago elongata Pursh (1774)
Plantago patagonica Jacq. (37)
Plantago virginica L. (2675)
Veronica peregrina L. (1967)

PLATANACEAE
Platanus wrightii S. Wats. (1642)

POACEAE
Aristida adscensionis L. (758)
Aristida havardii Vasey (2264)
Aristida purpurea Nutt. (167)
Aristida ternipes Cav. (892)
Bothriochloa barbinodis (Lag.) Herter (379)
**Bothriochloa ischaemum* (L.) Keng (670)
Bothriochloa springfieldii (Gould) Parodi (1179)
Bouteloua aristidoides (Kunth) Griseb. (666)
Bouteloua barbata var. *barbata* Lag. (164, 672)
Bouteloua barbata var. *rothrockii* (Vasey) Gould (668)
Bouteloua chondrosioides (Kunth) Benth. ex S. Wats. (1203)
Bouteloua curtipendula (Michx.) Torr. (970)
Bouteloua eriopoda (Torr.) Torr. (1202)
Bouteloua gracilis (Kunth) Lag. ex Griffiths (1095)
Bouteloua hirsuta Lag. (783)
Bouteloua radicosa (Fourn.) Griffiths (1069)
**Bromus catharticus* Vahl (2951)
Cenchrus spinifex Cav. (1348)
**Cenchrus ciliaris* L., *also Pennisetum ciliare* (L.) Link (2420)
Chloris virgata Sw. (804)
**Cynodon dactylon* (L.) Pers. (981)
Dasyochloa pulchella (Kunth) Willd. ex Rydb. (119)
Digitaria californica (Benth.) Henr. (677)
Dinebra viscida (Scribn.) P.M. Peterson & N. Snow (807)
Diplachne fusca ssp. *uninervia* (J. Presl) P. M. Peterson & N. Snow (1602)
Disakisperma dubium (Kunth) P.M. Peterson & N. Snow (734)
**Echinochloa colona* (L.) Link (1429)
**Echinochloa crus-galli* (L.) Beauv. (569)
Elymus elymoides (Raf.) Swezey (1954)
**Enneapogon cenchroides* (Licht.ex Roem. & Schult.) C.E. Hubb. (2479)
Enneapogon desvauxii Desv. ex Beauv. (1153)
**Eragrostis cilianensis* (All.) Vign. ex Janchen (802, 1599)

**Eragrostis curvula* (Schrad.) Nees (1488)
Eragrostis intermedia A.S. Hitchc. (1188)
**Eragrostis lehmanniana* Nees (221)
Eragrostis pectinacea (Michx.) Nees ex Steud. (1163)
Eriochloa acuminata (J. Presl) Kunth (1159)
Heteropogon contortus (L.) Beauv. ex Roemer & J.A. Schultes (621)
Hilaria belangeri (Steud.) Nash (523)
Hilaria mutica (Buckl.) Benth. (98)
Hopia obtusa (Kunth) Zuloaga & Morrone (508)
Hordeum pusillum Nutt. (2940)
Lycurus setosus (Nutt.) C.G. Reeder, also *Muhlenbergia alopecuroides* (Griseb.) P.M. Peterson & Columbus (1235)
Muhlenbergia arenacea (Buckl.) A.S. Hitchc. (2253)
Muhlenbergia emersleyi Vasey (1215)
Muhlenbergia fragilis Swallen (996)
Muhlenbergia pauciflora Buckl. (1226)
Muhlenbergia porteri Scribn. ex Beal (680)
Muhlenbergia repens (J. Presl) A.S. Hitchc. (1481)
**Panicum antidotale* Retz. (2511)
Panicum capillare L. (1089)
Panicum hirticaule J. Presl (2203)
Paspalum distichum L. (2426)
**Schismus arabicus* Nees (2950)
**Schismus barbatus* (Loefl. ex L.) Thellung (226, 1788)
Schizachyrium cirratum (Hack.) Woot. & Standl. (963)
Scleropogon brevifolius Phil. (1151)
Setaria leucopila (Scribn. & Merr.) K. Schum. (721)
Setaria macrostachya Kunth (278)
**Sorghum halepense* (L.) Pers. (549)
Sporobolus airoides (Torr.) Torr. (864)
Sporobolus contractus A.S. Hitchc. (1112)
Sporobolus cryptandrus (Torr.) A. Gray (2255)
Sporobolus pyramidatus (Lam.) C.L. Hitchc. (1607)
Sporobolus wrightii Munro ex Scribn. (1060)
Tragus berteronianus J.A. Schultes (1473)
Tridens muticus (Torr.) Nash (1191)
Trisetum interruptum Buckl. (2941)
Urochloa arizonica (Scribn. & Merr.) O. Morrone & F. Zuloaga (806)
Vulpia octoflora (Walt.) Rydb. (1870)

POLEMONIACEAE
Eriastrum diffusum (A. Gray) Mason (58)
Gilia mexicana A.& V. Grant (1915)
Gilia flavocincta subsp. australis (A.& V. Grant) Day & V. Grant (1793)
Ipomopsis longiflora (Torr.) V. Grant (200)
Leptosiphon chrysanthus J.M. Porter & R. Patterson (2859)
Linanthus bigelovii (A. Gray) Greene (2618)

POLYGALACEAE
Polygala barbeyana Chod. (144)
Polygala obscura Benth. (2763)

POLYGONACEAE
Eriogonum abertianum Torr. (81)
Eriogonum polycladon Benth. (825)
Eriogonum trichopes Torr. (213)
Eriogonum wrightii Torr. ex Benth. (849.1)
Persicaria bicornis (Raf.) Nieuwl. (2408, 1950)
**Polygonum argyrocoleon* Steud. ex Kunze (2507)
**Polygonum aviculare* L. (248)
Rumex hymenosepalus Torr. (89)

PONTEDERIACEAE
Heteranthera limosa (Sw.) Willd. (705)

PORTULACACEAE
Portulaca oleracea L. (2260)
Portulaca suffrutescens Engelm. (636)
Portulaca umbraticola Kunth (868)

POTAMOGETONACEAE
Potamogeton nodosus Poir. (1649)
Potamogeton foliosus Raf. (2788)

PRIMULACEAE
Androsace occidentalis Pursh (1681)

PTERIDACEAE
Astrolepis sinuata (Lag. ex Sw.) Benham & Windham (685)
Bommeria hispida (Mett. ex Kuhn) Underwood (526)
Myriopteris rufa Fée (126, 527)
Notholaena grayi Davenport (683)
Pellaea truncata Goodding (241, 528)

RANUNCULACEAE
Anemone tuberosa Rydb. (2568)
Clematis drummondii Torr. & A. Gray (1296)
Delphinium wootonii Rydb. (62)
Myosurus cupulatus S. Wats. (2660)
Myosurus minimus L. (288)

RHAMNACEAE
Ziziphus obtusifolia (Hook. ex Torr. & A. Gray) A. Gray (258)

ROSACEAE
Fallugia paradoxa (D. Don) Endl. ex Torr. (244)

RUBIACEAE
Houstonia rubra Cav. (454)

SALICACEAE
Populus fremontii S. Wats. (907)
Salix exigua Nutt. (2881)
Salix gooddingii Ball (2593)

SAPINDACEAE
Sapindus drummondii Hook. & Arn. (362)

SAPOTACEAE
Sideroxylon lanuginosum Michx. (1244)

SCROPHULARIACEAE
**Verbascum virgatum* Stokes (1957)

SOLANACEAE
Chamaesaracha coronopus (Dunal) A. Gray (112)
Chamaesaracha sordida (Dunal) A. Gray (656)
Datura wrightii Regel (277)
Lycium andersonii A. Gray (874)
Lycium pallidum Miers (324)
Nicotiana obtusifolia Mertens & Galeotti (103)
Physalis acutifolia (Miers) Sandw. (913)
Physalis angulata L. (2796)
Physalis hederifolia A. Gray (778)
Physalis solanacea (Schltdl.) Axelius (2388)
Solanum douglasii Dunal (954)
Solanum elaeagnifolium Cav. (163)
Solanum jamesii Torr. (2810)
Solanum rostratum Dunal (2876)

TALINACEAE
Talinum paniculatum (Jacq.) Gaertn. (840)

ULMACEAE
**Ulmus pumila* L. (838)

VERBENACEAE
Aloysia wrightii Heller ex Abrams (484)
Glandularia latilobata (L.M. Perry) Nesom, comb. et stat. nov. (52)
Verbena bracteata Lag. & Rodr. (249)
Verbena gracilis Desf. (344)
Verbena plicata Greene (606)

VIOLACEAE
Hybanthus verticillatus (Ortega) Baill. (140)

ZYGOPHYLLACEAE
Kallstroemia californica (S. Wats.) Vail (2329)
Kallstroemia grandiflora Torr. ex A. Gray (546)
Kallstroemia hirsutissima Vail ex Small (2795)
Kallstroemia parviflora J.B.S. Norton (718)
Larrea tridentata (Sessé & Moc. ex DC.) Coville (285)
**Tribulus terrestris* L. (674)

* denotes an introduced species

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NOTES ON THE BIOLOGY OF *ERIGERON DECRESCENS* (ASTERACEAE) OF SOUTHEASTERN ARIZONA

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ABSTRACT

Studies were conducted during 2020 to provide more detail concerning the biology of the newly described *Erigeron decrescens*. Several populations have been located in addition to the type locality and its range of more than 20 square miles in central Cochise County is mapped. One population is estimated to contain thousands of individual plants scattered over more than one hundred acres. *Erigeron decrescens* begins flowering later and ends earlier than *E. divergens* and *E. incomptus*, which are common in the same area. Scattered plants of *E. descrescens* develop as genetic mosaics, retaining the non-woody taproot, low habit, and discoid heads of *E. descrescens* while producing taller stems and radiate heads of *E. divergens*; other plants initially of *E. descrescens* morphology produce *E. incomptus* portions — with taller stems, radiate heads, and woodiness of the root and caudex.

Erigeron decrescens (Nesom & Roll 2020) was described based on collections made in April 2019 from the Pat Hills region of Cochise Co., Arizona. Studies continued during 2020 to provide more detail concerning its biology as well as to make a more complete assessment of its geographic range.

Four other *Erigeron* species occur in the desert grasslands of the Pat Hills area. Plants of *E. divergens* are annual and all appear to be variant no. 2 described by Nesom (2015; *Erigeron wootonii* Rydb., the earliest name). This variant has a multicipital caudex with stems arising from a caudex-like taproot apex. This multicipital caudex is similar to that in *E. decrescens*. *Erigeron incomptus* is distinct in its perennial duration, with a woody taproot and often with woody caudex branches — dead stems from the previous year often persist on early-season plants and basal leaves contrast with *E. divergens* and *E. decrescens* in their elongate petioles. *Erigeron arisolius* and *Erigeron canadensis*, both annuals, are also present in lesser numbers in the area.

Distribution

Several populations of *Erigeron decrescens* have been located and documented in addition to the type locality. The current range of the species covers more than twenty square miles (Fig. 1). One population is estimated to contain thousands of individual plants scattered over more than one hundred acres.

Ecology and associated species

The winter/spring precipitation at the type location in 2020 was average to above average. The Chiricahua National Monument (approximately 10 miles away) recorded 4.52 inches of rain between January 1 and June 15, with most of that falling before the end of March.

The type locality is a small draw in desert grassland just east of the Pat Hills. Within the draw are a number of wallows, or shallow depressions, that hold water after heavy rains. *Erigeron decrescens* was found along the edges of the wallows and in the lower portions of the extended draw. Additional populations have been discovered in low areas of grassland where the grass *Hilaria mutica* is dominant, and in other areas of grassland that are unusually wet. For instance, *E. decrescens* was

found growing at the margins of two cienega-like areas along former watercourses of Pine Creek, near the Chiricahua mountains.

Erigeron decrescens consistently occurs in close association with *E. divergens*. At the type locality, *E. incomptus* also is present in large numbers in the wetter bottoms of the wallows and other areas of the drainage where water collects.

The most common perennial associate of *Erigeron descrescens* is the grass *Hilaria mutica*. In addition to *E. divergens*, common annual associates include *Veronica peregrina*, *Plantago elongata*, *Plantago patagonica*, *Myosurus minimus*, *Androsace occidentalis*, and *Gamochaeta stagnalis*.

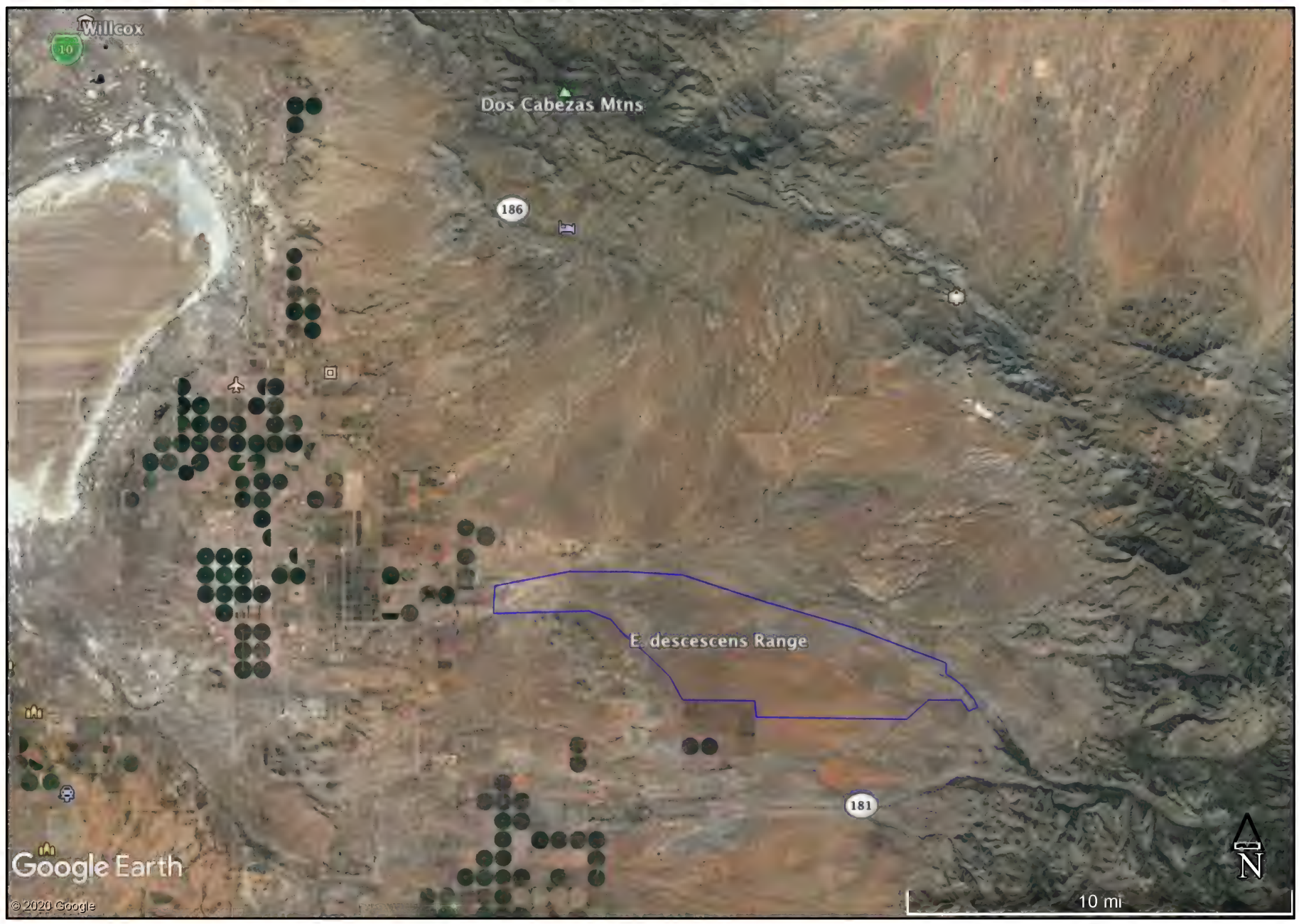

Figure 1. Estimated range of *Erigeron decrescens* in central Cochise County. The Chiricahua Mountains show as the high elevation on the east side.

Life cycle

Seedlings of *Erigeron decrescens* and *E. divergens* appeared in January and February after winter rainfall. The seedlings are difficult to tell apart but differences between the two species develop as they mature. Plants of *E. divergens* began to flower around March 15 and plants of *E. decrescens* began to flower around 1 April.

By the middle of March, plants of the two species began to show significant differences. Comparative field measurements were made of *Erigeron decrescens* plants and *E. divergens* plants growing in pairs within approximately 20 cm of each other at two different localities on April 16. The averages of these measurements are summarized below in Table 1.

	E. decrescens at type location	*E. divergens* at type location	*E. decrescens* at secondary location	*E. divergens* at secondary location
Laminae length	1.0 mm	4.6 mm	--	--
Pedicel width	1.9 mm	1.1 mm	1.6 mm	1.0 mm
Stem length	4.5 cm	10.5 cm	4.3 cm	11.7 cm
Involucre depth	3.7 mm	2.8 mm	2.6 mm	2.2 mm
Taproot width below caudex	4.9 mm	2.7 mm	2.9 mm	1.8 mm

Table 1. Comparative measurements of *Erigeron decrescens* and *E. divergens* on 16 April.

Erigeron divergens began to have elongating stems with nodding buds, while *E. decrescens* remained very short (3–5 cm) with erect buds. Plants of *E. divergens* maintained a blue-green color and their pedicels were slender (1–1.5 mm), tending to become darker and purplish beneath the heads. Plants of *E. decrescens* had a lighter, yellow-green color, with pedicels shorter, wider (1.5–2.5 mm), and straw colored.

The taproot of *Erigeron divergens* is slender, from 1.5–3.5 mm wide at the caudex and usually longer than those of *E. decrescens*. The taproot of *E. decrescens* is wider and expanded just below the caudex. Its width at the caudex measured between 2 and 6 mm, however in large plants can exceed 8 mm. From there it tapers rapidly, often giving the appearance of a small carrot.

Stems of *Erigeron divergens* ranged from 5.8 to 16 cm in height, reaching 35 cm or more in more mature plants later in the spring, and produced multiple heads. Stems of *E. decrescens* ranged from 2.4 to 8.5 cm, although they rarely exceed 5 cm and usually only have a terminal head (comparative size and morphology illustrated in Figs. 2 and 3). Ray corollas of *E. decrescens* have greatly shortened laminae (0 to 3 mm long) and their involucres are deeper (2.5 to 5.0 mm deep). Ray laminae of *E. divergens* measured from 4 to 6 mm long and involucres between 2.0 and 3.2 mm deep.

A plant of *Erigeron decrescens* and one of *E. divergens* growing side-by-side were identified with the field marker 8484. Figure 4 shows the two plants in the field on 16 April. Figure 5 shows the two plants after collection on the same date.

Figure 2. *Erigeron decrescens* (above) and *E. divergens* (below) growing less than 20 cm apart on 16 April 2020.

Figure 3. *Erigeron decrescens* (3 plants on left) and *E. divergens* (3 plants on right) on 16 April 2020.

Erigeron divergens began to have elongating stems with nodding buds, while *E. decrescens* remained very short (3–5 cm) with erect buds. Plants of *E. divergens* maintained a blue-green color and their pedicels were slender (1–1.5 mm), tending to become darker and purplish beneath the heads. Plants of *E. decrescens* had a lighter, yellow-green color, with pedicels shorter, wider (1.5–2.5 mm), and straw colored.

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A plant of *Erigeron decrescens* and one of *E. divergens* growing side-by-side were identified with the field marker 8484. Figure 4 shows the two plants alive in the field on 16 April. Figure 5 shows the two plants after collection on the same date.

Figure 4. *Erigeron decrescens* (left) and *E. divergens* (right), field marker 8484, before collection on 16 April.

Figure 5. *Erigeron decrescens* (upper) and *E. divergens* (bottom), field marker 8484, after collection.

At the end of April, most *Erigeron decrescens* plants began showing signs of water stress, overall desiccation, and browning of foliage. Nearby plants of *E. divergens* and *E. incomptus* were in full flower without indication of dessication and browning. By 26 May only one plant of *E. decrescens* remained in flower. Although some *E. divergens* plants were beginning to brown and shrivel, many were still green and in flower. *Erigeron incomptus* plants continued to flower and were not shriveling or browning. Figures 6 through 10 illustrate the differential senescence between *E. decrescens* and *E. divergens* at the type locality.

Figure 6. *Erigeron decrescens* (left) and *E. divergens* (right) on 6 May 2020.

Figure 7. *Erigeron decrescens* and *E. divergens* on 10 May 2020.

Figure 8. *Erigeron decrescens* and *E. divergens* on 20 May 2020.

Figure 9. *Erigeron decrescens* and *E. divergens* on 25 May 2020.

Figure 10. *Erigeron decrescens* completely desicated and *E. divergens* with reduced flowering on 17 June 2020.

Mature heads of *Erigeron decrescens* collected on 26 May had produced few fully formed achenes. Most achenes observed were dark and small (less than 0.4 mm long) or pale and misshapen. In contrast, mature heads collected on April 28 produced numerous, fully formed (approximately 0.8–1.0 mm long) achenes.

Flowering of *Erigeron decrescens* had stopped at the type locality completely by 2 June. *Erigeron incomptus* and *E. divergens* continued to flower beyond 15 June, but flowering had slowed and most of those plants were beginning to dry. Although some of the *E. divergens* plants had died, many were still alive as the summer monsoon season was about to begin in late June. *Erigeron arisolius* was observed in flower in April and May; *E. canadensis* had not flowered prior to 15 June.

Feb 15----Mar 1----Mar 15----Apr 1----Apr 15----May 1----May 15----June 1----June 15

Erigeron incomptus
I---------->
Erigeron divergens
I---------->
Erigeron decrescens
I----------I

Table 2. Flowering periods of *Erigeron* species at the type locality of *E. descrescens*.

Intermediates

From mid to late April, apparent genetic mosaics of *Erigeron decrescens* and *E. divergens* and of *E. decrescens* and *E. incomptus* (Figs. 11–13) were discovered in both of the larger populations of *E. descrescens*, indicating that *E. descrescens* is polyploid, apparently incorporating at least three genomes.

Figure 11. Apparent genetic mosaic of *Erigeron decrescens* and *E. divergens*, with *E. divergens*-like stems arising from a plant of *E. decrescens*, 16 April 2020.

In early growth, these showed only features of *E. decrescens*, but in mid April they began producing shoots characteristic of *E. divergens*. These divergens-like stems are 2–3 (or more) times longer than the decrescens-like stems and have leaves and flowers typical of *E. divergens* (Fig. 11 and Fig. 12, *Roll 2930*).

Figure 12. Apparent genetic mosaic of *Erigeron decrescens* and *E. divergens* (*Roll 2930*), collected on 30 April 2020.

On April 30, a mosaic was discovered with a woody root/caudex, long stems from the multicipital caudex, and stems of the previous year still attached (*Roll 2931*, Fig. 12), as in *E. incomptus*. Shorter stems and heads were those of *Erigeron decrescens* (Fig. 12). Similar *E. decrescens*/*incomptus* mosaics were observed in May at the type locality.

Figure 11. Apparent genetic mosaic of *Erigeron decrescens* and *E. incomptus* (*Roll 2931*), collected on 30 April 2020. The shorter stems and discoid heads are *E. descrescens*; radiate heads on taller stems and the woody root/caudex are *E. incomptus*.

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NOTE ON *ERIGERON DIVERGENS* AND *E. INCOMPTUS* (ASTERACEAE) IN THE SANTA CATALINA MOUNTAINS, ARIZONA

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I have been surveying vegetation in Finger Rock Canyon of the Santa Catalina Mountains at least twice monthly since 1984 (Bertelsen 2018) and 1743 field surveys have been completed to date. I did not distinguish between *Erigeron divergens* and *E. incomptus* until 2015, following the publication by Nesom (2015) on their distinction. This note places on record observations of *E. incomptus* and *E. divergens* in Finger Rock Canyon in early season 2020. Observations ended 8 June 2020 because of the 118,000+ acre Bighorn fire that has burned at least half of the canyon.

The six *Erigeron* species found in Finger Rock Canyon with their elevation ranges are as follows:

E. divergens (3100-5600 feet, with individual plants at 6000, 6450, and 7100 feet)
E. incomptus (3600-5550 feet)
E. lobatus (three plants at 3250 feet)
E. neomexicanus (6680-6900 feet, with a single plant at 6000 feet)
E. oreophilus (3500-7250 feet)
E. tracyi (5300-5700 feet).

The only location where more than two *Erigeron* species are found in close proximity is on a north-facing slope between 5200 and 5500 feet elevation, where *E. divergens* (uncommon), *E. incomptus* (common), *E. oreophilus* (common), and *E. tracyi* (uncommon) are usually found. *Erigeron oreophilus* commonly grows nearby all the other *Erigeron* species except *E. lobatus*. *Erigeron divergens* and *E. incomptus* are found in close proximity only on this north-facing slope — I have been unable to determine any preferred habitat or microhabitat differences between the two species.

Nearly all the *Erigeron divergens* plants observed in the canyon have been the multi-stemmed form described in Nesom (2015) (annual, with multiple, ascending stems from the base, all usually arising compactly from a caudex-like taproot apex; *E. wootonii* Rydb. the earliest name at species rank, fide G. Nesom). The single-stemmed form (typical, widespread *E. divergens*, annual, branching mostly above the base) has been seen only at the lower and higher end of the elevation range (in desert scrub and oak-pine woodland). The three plants found above 5600 feet elevation were single-stemmed, and all plants seen in desert scrub have been single-stemmed. These single-stemmed plants remained single-stemmed from the base throughout the season. My data on the single-stemmed form of *E. divergens* are scanty since it is very uncommon in Finger Rock Canyon, and I cannot say anything about its life history except that it appears to flower only in spring. In 2020, several marked plants of the multi-stemmed form of *E. divergens* initially were single-stemmed but produced several stems from the base after they began flowering. By contrast, *E. incomptus* begins to produce new stems as the plants begin to grow in spring, before flowering. I do not know whether they continue to produce new stems throughout the growing season or if stems die back to the root during cold winters.

Based on data collected from November 2015, the multi-stemmed form of *Erigeron divergens* and *E. incomptus* flower primarily in the spring (March-May) and again during the summer monsoon (August-September). The spring flowering season is longer and more productive, in terms of number of heads, than the monsoon flowering season. Both species, however, have been seen flowering every month of the year. The two species are similar in height, normally 12–16 inches, and inflorescence size. In Finger Rock canyon, the basal leaves of *E. divergens* are always spatulate and entire while

those of *E. incomptus* are always pinnatifid. I see no significant difference between the two species at any given time of year in the length of the rays, although the rays of both are nearly always shorter than those of *E. oreophilus*. On 8 June, I found several *E. incomptus* plants (a shaded site at 4450 feet elevation) with noticeably longer rays than those of plants higher up (and in sunny sites).

Inspection of the base of plants is necessary to distinguish between *Erigeron divergens* and *E. incomptus*. In spring, the spatulate basal leaves of *E. divergens* disappear soon after plants begin to flower, but the pinnatifid basal leaves of *E. incomptus* remain green for several weeks and dried-up fragments remain throughout the monsoon. Both species become largely dormant in June and much of July except in microhabitats, but green up with the onset of the rains. While dormant, the stems of both appear dead, but they quickly produce cauline leaves and flowers with the onset of the monsoon. New basal leaves are not produced by either species during the monsoon.

The 2019-2020 cool season (October-March) was characterized by above normal rainfall, but no rain fell until the last week in November. In my experience, November precipitation is essential for good growth of native annual species in spring; consequently I made a point of looking for annual seedlings in 2020. In general, native annuals did poorly but non-native annuals were abundant. Perennials, with a few exceptions, have had an exceptionally good flowering season.

After the mild winter, *Erigeron incomptus* began greening up in January and was first observed flowering on 10 February. Over the next couple of months, the number of stems and height of plants steadily increased and new plants appeared in large patches where I had not seen the species previously, suggesting that new plants germinated. This is certainly the most prolific year for *E. incomptus* since 2015, with more plants than I have seen before. In addition the stems of most plants were much longer (16–24 inches) than I have seen in previous years.

In contrast, *Erigeron divergens* is relatively uncommon and scattered this year and the plants are only about 16 inches high, perhaps because of a near absence of precipitation in November 2019. Seedlings of *E. divergens* were first recognized in mid-February. One plant in the bottom of the canyon, was first observed flowering on 9 March, but I did not see the species flowering at higher elevations until 13 April.

I regularly look for seedlings throughout the year, particularly at the beginning of the growing seasons, but I have not yet seen seedlings of *Erigeron incomptus*, perhaps because they are generally found in close proximity to mature plants. I have seen *E. divergens* seedlings in spring but not in summer.

After nearly five years of observing the *Erigeron incomptus* and *E. divergens*, I am convinced they are separate species. The morphological characteristics noted above have been consistent, and I have seen no evidence of hybridization or intergradation.

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RANGE OF *CYLINDROPUNTIA WHIPPLEI* (CACTACEAE) IN NEW MEXICO

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ABSTRACT

In New Mexico, *Cylindropuntia whipplei* is largely confined to the northwest quarter of the state. There are many documented localities from San Juan and McKinley counties, plus a few immediately to the east in Rio Arriba and Sandoval counties and south in Cibola and Catron counties. The species also is documented here from near the town of Gila, Grant County, far from other documented localities. A few other putative specimens of *C. whipplei* from New Mexico are questionably identified.

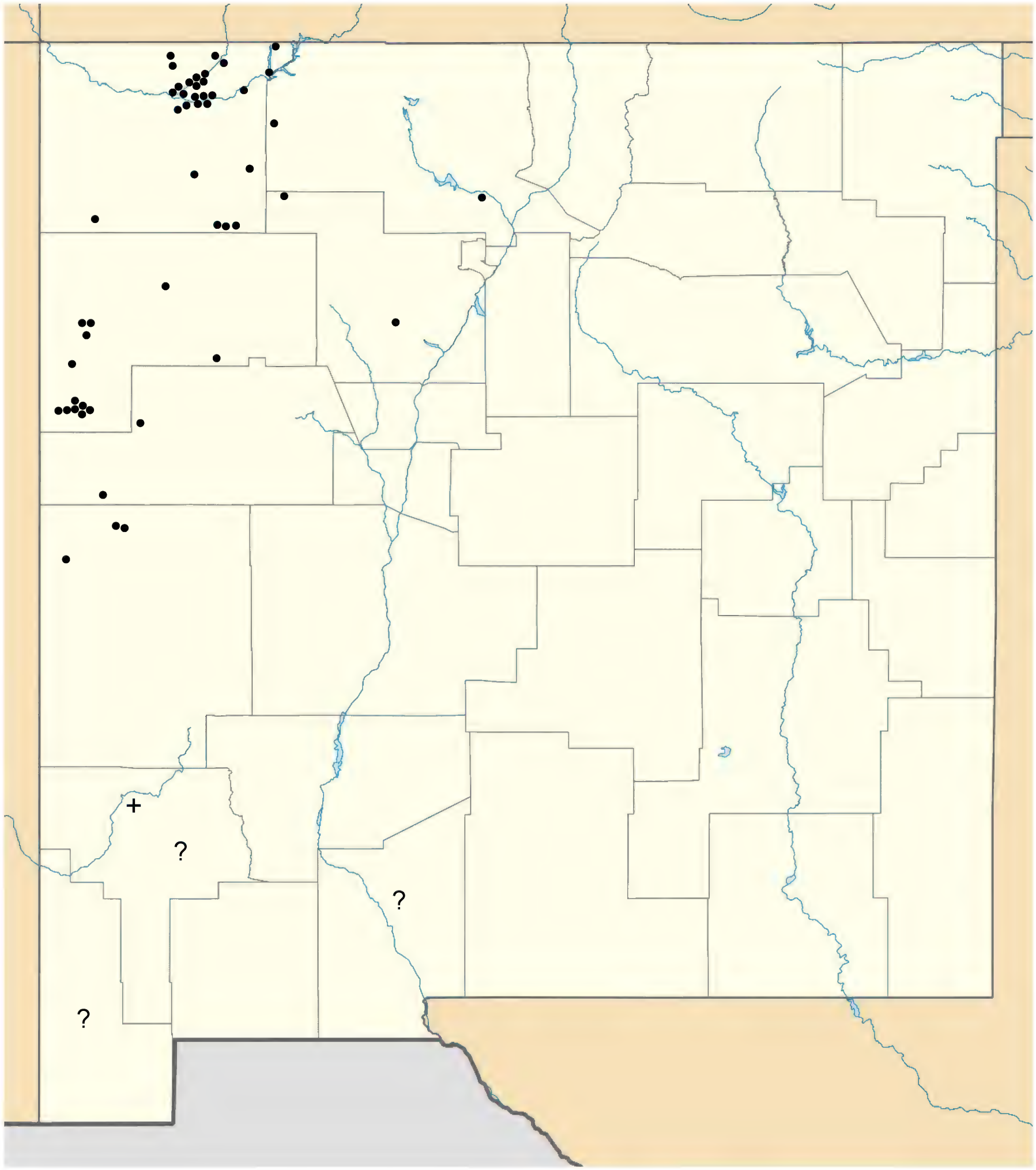
Cylindropuntia whipplei (Engelm. & J.M. Bigelow) F.M. Knuth var. *whipplei* is a relatively common species of cholla in the southwestern USA, with a center of distribution in the northern half of Arizona (Mohave, Yavapai, Coconino, Navajo, and Apache counties). It is easily visible along Interstate 40 between Seligman and Kingman (Figs. 1, 2) and along the South Rim by Grand Canyon Village. Its range extends short distances into adjacent Nevada, Utah, Colorado, and New Mexico, as well as short distances into southern Arizona (Gila Co.). This paper documents range limits of *C. whipplei* in New Mexico.

Figures 1 and 2. Ubiquitous *Cylindropuntia whipplei* var. *whipplei* along Interstate 40 in western Yavapai County, Arizona. These plants were much taller (~75 cm) and robust than the plant at Bear Creek.

Localities for vouchered specimens

In New Mexico, *Cylindropuntia whipplei* is well documented in both San Juan and McKinley Counties, plus a few specimens from just to the east in Rio Arriba and Sandoval counties and just to the south in Cibola and Catron counties. All those specimens are listed in Table 1 and on the map herein. Documented instances of *C. whipplei* in other New Mexico counties are equivocal (Table 2).

East of Sandoval County, Lyman Benson's (1982) distribution map shows *Cylindropuntia whipplei* in Santa Fe County. South of McKinley and Sandoval counties, Benson's map shows it in Cibola, Catron, Socorro, and Grant counties. Benson, however, provided scant documentation for these distribution points, listing only four herbarium records of *C. whipplei* for the entire state of New



Map 1. Herbarium specimens of *Cylindropuntia whipplei* in New Mexico

• = vouchered specimen of *Cylindropuntia whipplei*
? = vouchered specimen that has possibly erroneously been identified as *C. whipplei*
+ = new record of *C. whipplei* from Grant County

In order to show multiple herbarium specimens collected from well-collected sites, such as Farmington/Bloomfield/Aztec and from Zuni/Cheama Canyon, the points on the map are spaced slightly farther apart than if these were precisely at the collection coordinates. The blank New Mexico map with county borders and rivers is from Wikimedia Commons.

Mexico: Rio Arriba County; the town of Santa Fe; the town of Española, which straddles the border between Rio Arriba and Santa Fe counties; and Grant County. Benson's one record from the town of Santa Fe (*Pierce 2138*; UNM) clearly is of *C.* x *viridiflora* (Britton & Rose) F.M. Knuth, as annotated on the herbarium sheet by Nicole Trushell in 1984. I found only one other herbarium record for *C. whipplei* in Santa Fe County (Table 2), which is Benson's (1982) record from Española of a cultivated specimen in Santa Fe County (*V.O. Bailey s.n.*, US).

I found only two herbarium records for *Cylindropuntia whipplei* in Cibola County. These were from El Morro National Monument (*Rink 6070*, ASC) and Fence Lake (*Sivinski 3818*, UNM). Map 1 shows these and other vouchered records of *C. whipplei* in New Mexico.

Benson's (1982) record from Socorro County (1904, *Wooton 3008*; NMC) is actually from Catron County, at Puertocito, which is approximately ten kilometers (six miles) northwest of the town of Quemado. Until 1921, this portion of Catron County was part of Socorro County, which explains Benson's (1982) error regarding county. Another specimen was collected In 1994 from this same locale, El Portocito [note the slightly different spelling] (*Carter 1704*; UNM). There is one other documented locale for *C. whipplei* in Catron County, namely near Red Hill, 40 kilometers west-southwest of Quemodo (*Castetter 1031*; UNM). Marc Baker and Michelle Cloud-Hughes also recorded an observation of *C. whipplei* from near Red Hill (*Baker 18443*) on SEINet, but without a herbarium specimen deposited.

I have found only three vouchered specimens of *Cylindropuntia whipplei* in northern New Mexico from east of the Continental Divide, i.e. in the Rio Grande drainage (Map 1). One of these specimens is from near Prewitt in southeastern McKinley County, just north of the Cibola County border. Another specimen is from El Rito, along the Chama River in southeastern Rio Arriba County. The third specimen is from along Highway 550 (formerly Highway 44, until it was widened) northwest of San Ysidro, which is in south-central Sandoval County. The specimen from El Rito (*Rusby 145*; US) is fragmentary, consisting of only one pericarpel/fruit. It was collected in 1880 when *Opuntia whipplei* and *O. spinosior* were considered conspecific (see the next section). However, Marc Baker and Michelle Cloud-Hughes examined this specimen and identified it as *C. whipplei*. The specimen near San Ysidro (*Castetter 1978*; UNM) is from a well-travelled stretch of highway connecting Bernalillo and Bloomfield. In the early and mid 1990s along this stretch of highway, the only cholla species that I noticed were *C. imbricata*, often in huge stands, and *Grusonia clavata* (Engelm.) H. Rob. and *C. whipplei* has never again been collected from this locality.

Historical descriptions of range

The original description of *Cylindropuntia whipplei* fairly accurately described its range — "From the elevated country about Zuñi to the head of Williams's river" (Engelmann & Bigelow 1856, p. 51). Williams's River is now known as the Bill Williams River (U.S. Geological Survey 1980). The species now is known to be common north of the line between Zuni and the Bill Williams River, i.e. in Yavapai, Mojave, Coconino, Navajo, and Apache counties in Arizona, as well as into far southern portions of Colorado, Utah, and Nevada.

Engelmann (1856, p. 307) also mentioned *Opuntia whipplei*, "from Zuni…south to the Gila", but he was referring to *Opuntia whipplei* var. *spinosior* Engelmann, which is now often called *C. imbricata* (Haw.) F.M. Knuth subsp. *spinosior* (Engelm.) M.A. Baker, Cloud-H., & Majure [synonym *C. spinosior* (Engelm.) F.M. Knuth]. The original description of *Opuntia whipplei* (Engelmann & Bigelow 1856) distinguished the two varieties — var. *laevior* [as var. *lævior*] and var. *spinosior* — by var. *laevior* having shorter stems, shorter spines, and smaller seeds than var. *spinosior* and by var. *spinosior* being from south to the Gila whereas var. *laevior* being from between Zuni and the Bill Williams River. He was more specific with his description, writing that *C. whipplei* var. *laevior* "is from a few inches to 3-6 feet high; [while var. *spinosior*] forms small trees 8-10 feet high." In the

USA, the current known range of subsp. *spinosior* is from the Gila River watershed south to the Mexican border (Benson 1982; Pinkava 2003) — hence Engelmann's (1856) "south to the Gila" makes sense, although var. *spinosior* can also be found in northern parts of the Mimbres River watershed, in which *C. imbricata* subsp. *spinosior* starts to intergrade with *C. imbricata* subsp. *imbricata.* Engelmann (1859, p. 57) also wrote that the range of *Opuntia whipplei* var. *spinosior* was "From the Gila south to the Santa Cruz River and Tucson, and farther east." The phrase "the Gila" was and sometimes still is used to designate a fairly large area, such as the Mogollon-Datil volcanic fields.

Until Toumey (1898), *Cylindropuntia imbricata* subsp. *spinosior* was known as a variety of *Cylindropuntia whipplei*, under the name *Opuntia whipplei* var. *spinosior* Engelmann & J.M. Bigelow. This is important because the one herbarium specimen of *C. whipplei* from Grant County (*Blumer 155*, US) was collected soon thereafter, almost certainly between 1901 and 1905, and thus it would have been easy at the turn of the 20th century to conflate *C. whipplei* and *C. imbricata* subsp. *spinosior*.

Southern New Mexico: Hidalgo, Doña Ana, and Grant counties

In this section, I review three vouchered specimens from southern New Mexico that purportedly are *Cylindropuntia whipplei*. Because none of these specimens are yet digitized and because of the covid-19 pandemic, I have not yet seen photos nor scans of these three specimens.

There is a herbarium specimen labeled *Cylindropuntia whipplei* from the western edge of the San Andres Mountains on the Jornada Long-Term Ecological Research (LTER) site, formerly called the Jornada Ecological Range, in Doña Ana County (12 Dec 1934, *Engholm 799*, RM). I have not yet seen this specimen but it probably is either a small specimen of the locally common *C. imbricata* subsp. *imbricata* or possibly a rare hybrid of *C. imbricata* x *leptocaulis*. The Jornada LTER is an extensively studied research site from which there have been no other records or reports of *C. whipplei*, but *C. imbricata* subsp. *imbricata* and *C. leptocaulis* (DC.) F.M. Knuth are ubiquitous on the Jornada. As a graduate student in 1995-1996, I briefly studied on the Jornada but do not recall seeing *C. whipplei*. The specimen from the Jornada is odd in being in the Rio Grande drainage, i.e. east of the Continental Divide, as were specimens from near Prewitt in McKinley County, El Rito in Rio Arriba County, and near San Ysidro in Sandoval County.

Similarly, a collection identified as *Cylindropuntia whipplei* from just east-northeast of Animas, in central Hidalgo County (1985, *Worthington 13791*, UTEP) may be a small specimen of *C. imbricata* subsp. *spinosior* or possibly a hybrid of *C. imbricata* subsp. *spinosior* x *leptocaulis*. By contrast to the specimen from the Jornada, the Animas specimen is a more recent collection by someone who is familiar with both *C. imbricata* and *C. leptocaulis*.

Benson's (1982) distribution map shows two localities for *Cylindropuntia whipplei* in Grant County: Fort Bayard and a locale near Sherman, which is between San Lorenzo and Faywood. Benson's documentation only lists one specimen from Grant County, the specimen from Fort Bayard, the only specimen that I have found from Grant County. Nonetheless, while driving State Road 61 between San Lorenzo and Faywood and City of Rocks State Park, the only chollas I saw were *C. imbricata* (possibly subsp. *spinosior*) and a probably introduced *Grusonia emoryi* (Engelm.) Pinkava at City of Rocks.

There is a boxed specimen and label for *Blumer 155* of *Cylindropuntia whipplei* from Fort Bayard in Grant County. This collection was almost certainly made by J.C. Blumer during a summer between 1901 and 1905, when he was a seasonal summer worker for the U.S. Forest Service, partly in New Mexico, while an undergraduate at Iowa State College (Bowers 1983). And, as mentioned

above, *Blumer 155* was collected just after Toumey (1898) first published that *C. spinoisior* should no longer be considered a variety of *C. whipplei*.

On 11 March 2020, I visited Fort Bayard but did not find *Cylindropuntia whipplei*, despite this locale being flat with loose, deep, fine-grained soils, which is typical for *C. whipplei* in much of its range. The only cacti I found at Fort Bayard were numerous stunted specimens of *C. imbricata* subsp. *spinosior* and a few scraggly specimens of *Opuntia pottsii* Salm-Dyck. Fort Bayard is readily accessible and has been since it was established in the late 1860s, but no specimens of *C. whipplei* have ever been collected there, either before or after *Blumer 155*. I have found no other herbarium records of *C. whipplei* var. *whipplei* from Grant County, either vouchered or unvouchered. Thus, it is likely that no specimens of *C. whipplei* exist from Grant County. And, if the putative locales of *C. whipplei* from Hidalgo and Doña Ana counties are also equivocal, then the documented range of *C. whipplei* in New Mexico extends no farther south than northern portions of Catron County.

New locality near Gila in Grant County

With that background, I was surprised to find a native plant of *Cylindropuntia whipplei* var. *whipplei* near the Gila River in Grant County, approximately 8 km east of the town of Gila. By contrast, *C. imbricata* subsp. *spinosior* was abundant at this locality. The *C. whipplei* near Gila appeared to consist of a single clone growing 12 meters from Bear Creek (Figs. 3, 4), a major tributary of the Gila River that flows from near Piños Altos to the town of Cliff.

Figures 3 and 4. Clump of *C. whipplei* var. *whipplei* along Bear Creek, 8 km east of Gila, New Mex.

Figure 5. Underground horizontal woody shoot of *C. whipplei* along Bear Creek, with upright green shoots and vertical roots. The herbarium sheet was made from this specimen.

Figure 6. Skeletons of *C. whipplei* along Bear Creek, surrounding the main clump.

The clonal nature of this plant was suggested by several nearby plants connected to the main clump by prone shoots growing just below the soil surface. Sometimes these prone shoots looked like dead skeletons but were still alive (Fig. 5). Other times, both the prone shoots and the vertical aboveground shoots arising from them were clearly dead (Fig. 6). Despite extensive searches, I found no other nearby plants of *Cylindropuntia whipplei*.

The main clump of this plant was 18 cm tall and 43 cm in diameter. The entire diameter of the clump, including underground attached satellite shoots, was approximately 1 m. This plant had cladodes to 15 cm long, but most cladodes were much shorter. Cladodes were dark green, with transverse creasing in winter. Upright cladodes were 5-8 mm in diameter (Figs. 7, 8), but some older cladodes lying horizontally just below the soil surface with thick periderms were up to 25 mm in diameter (Figs. 5, 9, 10). Roots were sparsely branched, mostly vertical, and about 2-4 mm in diameter. I saw no shallow horizontally spreading roots just below the soil surface, as occurs in many cacti. Tubercles were raised and longer than wide, but tubercles were only obvious near the 'canopy' of this plant, which was where spines were present. Tubercles were virtually non-existent on lower parts of cladodes, which lacked spines, so that lower portions of cladodes appeared perfectly cylindrical. There was at most one spine per areole. Spines were only found at the 'canopy' of the plant, which meant the top centimeter, on areoles residing on raised tubercles. Some areoles residing on raised tubercles lacked spines or had very short spines that were under 4 mm long. The longer spines at the 'canopy' of this plant were 18-23 mm long, with white sheaths. Areoles were circular, 1.0-1.5 mm in diameter, with white glochids.

Figures 7 and 8. Close-up of terminal shoots ('canopy') of *C. whipplei* along Bear Creek.

Figures 9 and 10. The herbarium sheet from Bear Creek was made from this specimen of *C. whipplei*.

This plant was growing just south of a small (1.2 m tall) *Prosopis glandulosa* (mesquite), with a medium-sized (3 m tall) *Juniperus deppeana* (alligator juniper) overtopping the mesquite. This was a fairly shaded site. The substrate was composed of mesquite leaflets and juniper leaves above a layer of sand and gravel deposited by rare vernal flooding on nearby Bear Creek and rolling down the nearby hill that was 200 m tall. Other plants within 100 meters included *Platanus wrightii, Populus freemontii, Salix exigua, Quercus sp., Senagalia greggii* [*Acacia greggii*], *Pinus edulis, Yucca elata, Cylindropuntia imbricata* subsp. *spinosior, Echinocereus fendleri, Mammillaria wrightii*, *Opuntia macrocentra*, and *Opuntia phaeacantha*.

On 4 March 2020, I collected a specimen (Figs. 5, 9, 10) for the Dale A. Zimmerman Herbarium (SNM), from which the curator, William Norris, kindly prepared a herbarium sheet. This locality for this specimen is Grant County, 8 km E of Gila, 150 Double E Ranch Road, along Bear Creek, (32° 58' 33" N; -108° 30' 47" W [32.975833° N; -108.513056° W]), elev. 1458 meters. This locality is over 160 km (100 miles) from the vouchered specimens of *Cylindropuntia whipplei* from northern Catron County.

After showing this specimen of *Cylindropuntia whipplei* along Bear Creek to the property owners, one of them (Debbie Eggleston) commented that they have seen plenty of these plants before on their adjacent cattle ranch. She has had to remove them from their horses' feet. She also thought nothing of these other plants, believing that they were merely juvenile specimens of the ubiquitous *C. imbricata* subsp. *spinosior*. She was somewhat justified in this assessment insofar as young seedlings or even the first shoots sprouting from small fallen cladodes of *C. imbricata* subsp. *spinosior* have new shoots that superficially resemble those of *C. whipplei*. But entire mature plants of *C. whipplei* do not look like *C. imbricata* subsp. *spinosior*. Their skeletons also look different (Fig. 6).

I also asked the owners if it was possible that this lone individual of *Cylindropuntia whipplei* along Bear Creek could have arrived via a cladode being washed down the creek during vernal flooding. The other owner (Alan Eggleston) said this was highly unlikely because the hundred-year flood line was at least five meters closer to the creek, pointing to a line of different looking soil created by cottonwood and sycamore leaves that had been washed downstream. The winter of 2019/2020 had been quite wet, with decent snowpack in the Mogollon Mountains, and yet Bear Creek was still far from this *C. whipplei*. Of course, such a detached cladode could have traveled downstream in a spring flood and then later been transported by animal the remaining 5-10 m to its current location. Regardless, it would be interesting to find whether *C. whipplei* is present upstream from this locale on Bear Creek.

Conclusion

Cylindropuntia whipplei seems to be extremely rare or non-existent in New Mexico other than in the northwest quarter of the state. In New Mexico, *C. whipplei* is primarily found in the northwest quarter of the state, in the watersheds of the San Juan, Rio Puerco of the West, and Zuni Rivers, all of which are tributaries of the Little Colorado River. There are a few specimens of *C. whipplei* from northern Catron County, the one specimen described herein from east of the town of Gila, and a few specimens on the Atlantic side of the Continental Divide along western portions of the Rio Grande watershed, such as the specimens from Prewitt (McKinley County), San Ysidro (Sandoval County), and El Rito (Rio Arriba County).

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Table 1. Herbarium records of *Cylindropuntia whipplei* from New Mexico

County	Collection #	Date	Location	Lat.	Long.	Elev.	Herbaria
Catron							
	Wooton 3008	1904-05-25	Puertocito, NW Quemado †	34° 23’	108° 34’	1951	NMC, US
	Carter 1704	1994-08-01	El Porticito, NW Quemado	34° 23’	108° 34’	1951	UNM
	Castetter 1031	1962-06-20	Red Hill	34° 13’	108° 53’	2133	UNM
Cibola							
	Rink 6070	2007-06-04	El Morro National Mon.	35° 02’	108° 21’	2190	ASC, UNM
	Sivinski 3818	1997-06-19	Canyon Springs, Fence Lake	34° 45’	108° 51’	2014	UNM
Rio Arriba							
	Rusby 145	1880-08-01	El Rito	36° 20’	106° 11’	2102	US
	Holmes 81	1995-04-09	Largo Canyon, Crow Cyn	36° 23’	107° 31’	1981	SJNM
Sandoval							
	Heil 8715	1995-04-05	Counselor	36° 04’	107° 26’	2141	SJNM
	Castetter 1978	1963-06-23	9 km NW of San Ysidro	35° 34’	106° 52’	1725	UNM
McKinley							
	Bigelow s.n.	1853-11-22	Zuni	35° 05’	108° 47’	1951	RSA, POM, MO
	Pierce 1084	1962-07-18	Zuni	35° 05’	108° 44’	1950	UNM
	Camazine 115	2017-10-18	Zuni	35° 04’	108° 51’	1917	COLO

	Tierney s.n.	1981-06-14	Zuni, 7 km E of Zuni	35° 05’	108° 43’	2005	NMC
	Castetter 375	1954-08-07	9 km NE of Zuni	35° 14’	108° 46’	2200	UNM
	Baker 16670.2 *	2008-03-11	Cheama Canyon	35° 04’	108° 46’	2040	ASU
	Baker 17829.3	2013-10-26	Cheama Canyon	35° 04’	108° 43’	2050	ASU
	Baker 13815	2000-06-06	Cheama Canyon, east fork	35° 04’	108° 71’	2055	SD
	Peabody 1054	1977-05-17	Two Wells	35° 20’	108° 48’	2225	BRY
	Heil 9948	1996-05-13	Standing Rock	35° 48’	108° 20’	1966	SJNM, COLO
	Toumey s.n.	1896-10-06	Gallup	35° 32’	108° 45’	1987	US
	Eastwood 5618	1916-06-14	Gallup	35° 32’	108° 45’	1987	CAS
	Pierce 1084	1962-07-18	10 km S of Gallup	35° 05’	108° 43’	2133	UNM
	Baker 11732.1	1995-04-07	2 km SW of Prewitt	35° 22’	108° 03’	2134	US, UTEP, ASU
San Juan							
	Standley 7013	1911-07-18	Farmington	36° 40’	108° 12’	1600	US
	Standley 7128	1911-07-20	Farmington	36° 40’	108° 12’	1600	US
	Brass 14352	1940-06-17	Farmington	36° 40’	108° 12’	1524	GH
	Faulkner 143	1977-06-22	6 miles S of Farmington	36° 35’	108° 12’	1890	FLD
	Baker 11730	1995-04-06	SE of Farmington	36° 46’	108° 07’	1838	UCR
	Standley 8024	1911-08-16	Cedar Hills	36° 58’	107° 52’	1900	US
	Baker 13819	2000-06-09	2 km SE of Cedar Hills	36° 55’	107° 53’	1890	SD
	Pierce 1154	1962-08-16	3 km S of La Boca, CO	36° 59’	107° 36’	1981	UNM
	Harris 3432	1958-08-25	Navajo Lake (underwater)	36° 50’	107° 37’	1820	UNM
	unknown	1983-03-15	Turley	36° 44’	107° 47’	1900	UTEP
	Spellenberg 6560	1982-06-04	4 miles N of La Plata	36° 59’	108° 11’	1880	NMC
	Pierce 1028	1962-06-14	S of La Plata	36° 55’	108° 12’	1770	UNM
	Heil 4080	1972-01-08	1 mile W of Nageezi	36° 16’	107° 50’	2090	UNM
	Hibben 1983	1963-06	Chaco Canyon	36° 04’	107° 58’	1981	UNM
	Kass 1488	1983-10-16	Chaco Culture NHP	36° 04’	107° 58’	1981	BRY
	Koehler 17	1980-07-08	4 km E Chaco Culture NHP	36° 03’	107° 48’	1950	UNM
	Spellenberg 4122	1976-06-09	Black Lake, 15 mi SE Bisti	36° 11’	108° 04’	1890	NMC
	Clark 15347	1950-06-01	E Aztec, Animas River	36° 50’	108° 00’	1750	UNM
	Castetter 403	1980-07-08	Aztec	36° 50’	108° 00’	1750	UNM
	Rink 5053	2006-08-27	Aztec Ruins National Mon.	36° 50’	108° 00’	1750	ASC, UNM
	Rink 5976	2007-05-26	Aztec Ruins Natl. Mon.	36° 50’	108° 00’	1770	ASC, UNM
	Reeves 2186 **	1963-10-18	NE Bloomfield	36° 42’	108° 02’	1646	UNM
	Reeves 3196	1966-03-08	NE Bloomfield	36° 42’	108° 02’	1646	UNM
	Reeves 2217	1963-10-10	Bloomfield	36° 42’	108° 02’	1646	UNM
	Pierce 1492	1963-01-31	Bloomfield	36° 43’	107° 59’	1646	UNM
	Bohrer 1600	1972-06-30	Bloomfield, N Salmon Ruin	36° 42’	108° 02’	1646	RSA
	Pierce 3167	1965-10-11	5 miles W of Naschitti	36° 03’	108° 49’	2300	UNM
	Baker 478	1898-05-02	Aztec	36° 50’	108° 00’	1676	RM, NMC, MO, GH, NY

* On that same day, Marc Baker and Rafael Rouston collected three additional specimens of *Cylindropuntia whipplei* from the same locale: *Baker 16670.4* (ASU), *Baker 16670.7* (ASU), *Baker 16670.9* (US).

** On that same day, Bob Reeves collected an additional specimen of *C. whipplei* from the same locale: *Reeves 2187* (UNM).

† Portocito and Quemado were in Socorro County until 1921 when Catron County was split off from Socorro County.

Table 2. Questionable herbarium records and one new record of *C/ whipplei* from New Mexico

County	Collection #	Date	Location	Lat.	Long.	Elev.	Herb.
Santa Fe	*Bailey s.n.*	1904-10-19	Española - cultivated	36° 00’	106° 04’	1706	US
Doña Ana	*Engholm 799*	1934-12-12	Jornada LTER	36° 46’	106° 35’	1524	RM
Hidalgo	*Worthington 13791*	1985-10-12	1.1 km ENE of Animas	31° 57’	108° 47’	1340	UTEP
Grant	*Blumer 155*	*	Fort Bayard	32° 48’	108° 09’	1867	US *
Grant	*Gorelick s.n.*	2020-03-04	Gila, 8 km E of	32° 59’	108° 31’	1458	SNM §

* Robert ‘Bort’ Edwards at the Smithsonian has promised to provide me with a photo of the boxed specimen and label for *Blumer 155* from Fort Bayard once he is cleared to return to the workplace following the covid-19 pandemic quarantines. No herbarium sheet exists for this specimen, which is why it has never been digitized. Blumer only worked in New Mexico during summers from 1901-1905.

§ Bill Norris will complete this herbarium sheet following the covid-19 pandemic quarantines, based on a specimen (Figs 5, 9, 10) that I collected on 4 March 2020 and provided to him on 10 March 2020.

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NOTES ON THE DISTRIBUTION OF *ENEMION BITERNATUM* (RANUNCULACEAE) IN TEXAS

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ABSTRACT

Collections *Enemion biternatum* in Sabine and San Augustine counties of eastern Texas extend its known range by approximately 260 kilometers. It was previously known in Texas from a single population in Red River County.

Prior to 1998, *Enemion biternatum* Raf. (*Isopyrum biternatum* (Raf.) Torrey & Gray) was included in various floras of Texas including Correll & Johnston (1970), Hatch et al. (1990), and Jones et al. (1997). The inclusion by Correll and Johnston was based on a specimen collected by Charles Wright. They estimated the distribution as "possibly in n.e. Texas," which was the closest area within the state to existing populations in southeastern Oklahoma and southwestern Arkansas. Singhurst et al. (1998) speculated that the specimen was more likely from southeast Texas. All available accounts of Wright's travels through the region indicate that he would have entered the state via the El Camino Real (in Sabine County) and travelled to either San Augustine or Nacogdoches. From there he appears to have traveled to Angelina, Tyler, Jasper, and Newton counties, where he worked as a land surveyor from 1837 to 1845 (Geiser 1948). He was said to have spent time around Town Bluff in Tyler County and Zavalla in Angelina County. In Geiser's review of Wright's correspondence with Asa Gray there is no mention of time spent in northeast Texas.

In 1998 a population of *Enemion biternatum* was discovered in Red River County (Singurst et. al. 1998), occurring on Roebuck clay soils (Thomas 1977) in a hardwood forest near the base of a steep bluff. It was growing under a canopy of *Carya illinoinensis*, *Quercus macrocarpa*, *Q. muhlenbergii*, *Q. shumardii,* and *Populus deltoides*. Associated herbaceous species included *Carex* spp., *Erythronium albidum*, *Polygonatum biflorum*, *Impatiens capensis*, *Podophyllum peltatum*, *Parietaria pennsylvanica*, *Polygonum virginianum*, *Ranunculus* sp., *Sanicula canadensis*, *Smallanthus uvedalia*, and *Verbesina virgnica*.

A second population was discovered in 2016 by Matt Buckingham and Carolina Paez while surveying a rich calcareous hardwood forest in Sabine County. This population was visited by Buckingham and Jason Singhurst in 2017 and a collection of *E. biternatum* was made. Buckingham and Paez subsequently discovered a third population in 2020 in a floodplain forest in San Augustine County. These sites extend the known range of *Enemion biternatum* in Texas by approximately 260 kilometers.

Vouchers. **Texas**. Sabine Co.: Ca. 0.85 mi E of the intersection with SH 87 and Reeves Road on a moderately steep (5-15%) calcareous slope above Reeves Creek and Toledo Bend Reservoir, 6 Mar 2017, *Singhurst & Buckingham 22295* (BAYLU). San Augustine Co.: Floodplain forest on E side of Ayish Bayou and N side of SH 103, 0.54 mi E of the intersection of SH 103 and FM 705, 16 Feb 2020, *Buckingham & Paez s.n.* (BAYLU). Figures 1-4.

The Sabine County population occurs on a moderately steep slope in a rich hardwood forest on Eastwood very fine sandy loam soils (Griffith 2006). The canopy is dominated by *Fraxinus americana*, *Liquidambar styraciflua*, *Quercus pagoda*, *Q. shumardii*, and *Q. nigra*. Subcanopy woody plants include *Cercis canadensis*, *Acer leucoderme*, *Ostrya virginiana*, and *Crataegus* spp. Associated herbaceous species include *Carex albicans*, *Luzula echinata*, *Asplenium platyneuron*, *Claytonia virginica*, *Galium* spp., and *Podophyllum peltatum*. At this site, *E. biternatum* occurs with several other species of spring ephemeral forbs that are rare in the region including *Erythronium rostratum*, *Trillium gracile*, *Cardamine concactenata*, and *Phlox divaricata*. Adjacent slopes contain additional rare and noteworthy species including *Sanguinaria canadensis*, *Polygonatum biflorum*, *Spigelia marilandica*, *Fragaria virginiana*, *Lilium michauxii*, *Tipularia discolor*, and *Silene stellata*.

The location of the San Augustine County population contains a markedly different plant community. There the species occurs in a flat floodplain forest on the Mattex-Iulus soil complex, which consist of loams associated with areas of frequent flooding (Griffith 2006). The overstory contains a mix of typical floodplain hardwoods including *Quercus phellos*, *Q. lyrata*, *Ulmus rubra*, and *Celtis laevigata*. In some instances, *Enemion biternatum* was observed growing within close proximity to *Taxodium distichum*. Associated herbaceous species at this site include *Arundinaria gigantea*, *Carex spp.*, *Packera glabella*, *Viola sororia*, *Ranunculus sp.*, and *Cardamine bulbosa*.

The discovery of these populations helps confirm the belief that the Wright collection was not made in northeast Texas (although it is now known to occur there, i.e., Red River Co.), but rather further south in the Pineywoods (Singhurst et al. 1998). Considering that Wright entered Texas on the El Camino Real and subsequently traveled south and west to Angelina and Tyler counties, it is likely that his route would have crossed Ayish Bayou and other area streams that likely contained suitable habitat for *Enemion biternatum*. It is expected that the species is present in other areas in far east Texas that contain remnant mature hardwood forests over calcareous substrates.

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We extend our heartfelt thanks to Viron Barbay and Susan McCulley for inviting us to their property and for their exceptional stewardship that has allowed *E. biternatum* and other peripheral flora rare in Texas to thrive. We also thank Jared Barnes and Adam Black for thoughtful manuscript reviews.

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Figure 1. *Enemion biternatum* (Ranunculaceae) in Sabine County. Photo by Matt Buckingham.

Figure 2. *Enemion biternatum* in San Augustine County. Photo by Matt Buckingham.

Figure 3. Rich calcareous slope forest in Sabine County, with *Enemion biternatum, Erythronium rostratum,* and *Cardamine concactenata*. Photo by Matt Buckingham.

Figure 4. Floodplain forest in San Augustine County, with *Enemion biternatum*, *Cardamine bulbosa*, and *Ranunculus* spp. Photo by Matt Buckingham.

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TAXONOMIC CHANGES IN NORTH AMERICAN CAMPANULOIDEAE (CAMPANULACEAE)

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ABSTRACT

Recent phylogenetic studies conclude that *Campanula* is polyphyletic and that all but one of the native North American species of Campanuloideae belong in the *Rapunculus* clade of *Campanula*; within the *Rapunculus* clade they fall into five different subclades, three of which also contain other genera. In preparing the treatment of Campanuloideae for Flora of North America, it has become apparent that these "*Campanula*" species should be reclassified, and it is preferable that their morphology, ecology, and distribution be taken into account for their reclassification. To that end, here six new genera are established, one is reinstated with a new name, and one is elevated from subsection rank, to accommodate the taxa in clades predominantly of other genera: **PROTOCODON** Morin, **gen. nov.**, containing ***Protocodon robinsiae*** (Small) Morin, **comb. nov.**; **PALUSTRICODON** Morin, **gen. nov.**, containing ***Palustricodon aparinoides*** (Pursh) Morin **comb. nov**.; **EASTWOODIELLA** Morin, **gen. nov.**, containing ***Eastwoodiella californica*** (Kellogg) Morin, **comb. nov.**; **RAVENELLA** Morin, **gen. nov**, comprising four species, ***Ravenella exigua*** (Rattan) Morin, **comb. nov**., ***Ravenella angustiflora*** (Eastw.) Morin, **comb nov**., ***Ravenella griffinii*** (Morin) Morin **comb. nov**., and ***Ravenella sharsmithiae*** (Morin) Morin, **comb. nov.**; **SMITHIASTRUM** Morin, **gen. nov**., comprising ***Smithiastrum prenanthoides*** (Durand) Morin, **comb. nov**., and ***Smithiastrum wilkinsiana*** (Greene) Morin**, comb. nov**.; **POOLEA** Morin, **gen. nov.**, containing ***Poolea reverchonii*** (A. Gray) Morin, **comb. nov.**; and **ROTANTHELLA** Morin, **nom. nov.,** replacing *Rotantha* Small for the one species ***Rotanthella floridana*** (S. Wats. ex A. Gray) Morin, **comb. nov**. **MELANOCALYX** (Fed.) Morin, **stat. nov.**, is elevated to generic status and contains ***Melanocalyx uniflora*** (L.) Morin, **comb. nov**.

Campanuloideae Burnett (Campanulaceae Juss.) contains more than 1,000 species in some 50 genera worldwide, with most occurring in Africa, Asia, and Europe (Lammers 2007). *Campanula* L. is the largest genus in the subfamily, comprising 420 species (Lammers 2007) to 500 species (Contandriopoulos 1984). The treatment by Alphonse de Candolle (1830) is still the only worldwide monograph of Campanulaceae (he treated Campanulaceae and Lobeliaceae as separate families, as do many other authors), and there are few recent works that comprehensively treat even an entire genus throughout its range (e.g., *Codonopsis* and allied genera, Hong 2015). Campanuloideae has been the subject of a number of phylogenetic analyses (e.g., Eddie et al. 2003; Cosner et al. 2004; Borsch et al. 2009; Cellinese et al. 2009; Haberle et al. 2009; Roquet et al. 2009; Wendling et al. 2011; Mansion et al. 2012; Crowl et al. 2014; DeChaine et al. 2014; Crowl et al. 2016; Yoo et al. 2018). Some phylogenetic studies have focused on individual genera (e.g., *Phyteuma* L., Schneeweiss et al. 2013), species groups (e.g., isophyllous *Campanula,* Park et al. 2006), tribes or sections (e.g., Peracarpeae, Zhou et al. 2012; sect. *Quinqueloculares*, Eddie & Ingrouille 2008), biological characters (e.g. floral evolution, Crowl et al. 2016; stem anatomy, Schweingruber et al. 2014), or on geographical regions (e.g., Macaronesia, Menezes et al. 2018; Greece, Cellinese et al. 2009; Asia, Yoo et al. 2018). As the number of taxa sampled has increased, the phylogenies have been increasingly consistent, at least for the North American taxa. Mansion et al. (2012) characterized 17 clades within Campanuloideae that have continued to provide a backbone for subsequent work. These studies all agree that *Campanula,* as currently constituted, is polyphyletic.

McVaugh (1948), discussed the difficulties in defining genera within Campanulaceae. He noted that genera in Campanulaceae should be based on their coherence as biological units sharing combinations of characters not otherwise found in the family, emphasizing similarities and affinities among the members of the genus rather than differences from other genera. Lakuŝić et al. (2019) discussed this as a well-known taxonomic problem prevalent in Campanulaceae, noting "many of the genera cannot be diagnosed explicitly by single characters, but instead by a combination of them, or by overall appearance (*Gestalt*), often in combination with geographic distribution." Liveri et al. (2019) concluded "*Campanula* is not a natural entity and its complex historical evolution is hard to reconstruct even with molecular tools."

Historically, the North American taxa of Campanuloideae have been placed in four to eight genera, including *Campanula*. Shetler (1963) provided an overview of native and naturalized *Campanula* in North America. Rosatti (1986) gave a more in-depth discussion of the taxa in the southeastern USA. Most phylogenetic studies have included at least some North American taxa. Wendling et al. (2011) focused on taxa in western North America, including 21 North American species in their analysis; DeChaine et al. (2014) documented radiation of the seven arctic-alpine campanulas in western North America. Yoo et al. (2018), in their work on the origins of Asian Campanulaceae, included 24 North American species as well as more than half of the east Asian taxa.

Following Eddie et al. 2003, these molecular studies have consistently identified two major clades in Campanuleae Dumort. (Hong & Wang 2015): *Campanula* in the strict sense, and the Rapunculus clade. The monotypic Asian *Peracarpa* Hook f. & Thoms. is sister to the Rapunculus clade (Yoo et al. 2018).

All but one species (*Campanula chamissonis* Fed.) of North American Campanuleae are in the Rapunculus clade (Eddie 1997; Eddie et al. 2003). Wendling et al. (2011) distinguished two clades within the Rapunculus clade: Rapunculus 1 and Rapunculus 2. Yoo et al. (2018) and Wendling et al. (2011) sampled slightly different taxa — their combined results suggest that within the *Rapunculus* clade, North American taxa fall into two superclades:

1. Wendling et al.'s Rapunculus 1 contains species still considered *Campanula*. In Rapunculus 1A are the generally mountain-dwelling North American species *C. parryi* A. Gray, *C. scabrella* Engelm., *C. aurita* Greene, *C. divaricata* Michx., *C. lasiocarpa* Cham., and *C. piperi* Howell. Although *Campanula scouleri* Hook. ex A. DC. is shown as sister to *C. prenanthoides* in Rapunculus 2A of Wendling et al.'s cladogram, that is due to a misidentification. It is correctly placed in Rapunculus 1. *Campanula shetleri* Heckard would be expected to fall here. Yoo et al. 2018 showed these Cordilleran, high elevation western species nested within the *Campanula isophylla* Moretti clade. All are western species except the Appalachian *C. divaricata*. *Campanula rotundifolia* L., a circumboreal perennial, is in a distant subclade of taxa, Wendling et al.'s Rapunculus 1B, all of which are still in *Campanula* (Yoo et al. 2018).

2. Wendling et al.'s Rapunculus 2 has three subclades. *Rapunculus* 2A contains these North American taxa: *Campanula robinsiae* Small, *C. aparinoides* Pursh, *C. exigua* Rattan, *Githopsis* Nutt., *Heterocodon* Nutt., *Campanula wilkinsiana* Greene, and *C. prenanthoides* Durand. Mansion et al. 2012 placed *C. californica* (Kellogg) A. Heller and *C. angustiflora* Eastw. here. The second subclade (Wendling et al.'s Rapunculus 2B) contains *Campanulastrum* Small, *Campanula reverchonii* A. Gray, *Triodanis* Raf., and *Campanula floridana* S. Wats. ex A. Gray (together sister to the non-North American *Legousia*). Yoo et al. (2018) placed Eurasian *Campanula pterocaula* Hausskn., *C. stevenii* M. Bieb., and *C. persicifolia* L. as sister to this second subclade. A third subclade (Wendling's *Rapunculus* 2C) contains North American *Campanula uniflora* L. associated with the non-North American genera *Petromarula* Vent. ex Hedwig fil., *Asyneuma* Griseb. & Schenk, *Physoplexis* (Endl.) Schur, and *Phyteuma* L.

In North America in particular, the most egregious problems in Campanuloideae are with the Rapunculus 2 clades, within which species still treated as *Campanula* are embedded. These "campanulas" are distinctive in their morphology, ecology, and geographic distribution, and maintaining them as *Campanula* within the other 400+ species obscures their relationships and history.

The Cordilleran, arctic-alpine *Campanula* species in Wendling et al.'s (2011) Rapunculus 1 clade (*Campanula lasiocarpa*, *C. scabrella*, *C. parryi*, *C. piperi*, *C. shetleri*, *C. aurita*, *C. scouleri*, and the Appalachian *C. divaricata*) and *Campanula rotundifolia* should also be placed in a different genus or different genera; because these species are embedded in a large clade of Eurasian species it seems better to wait until the entire group has been studied before making nomenclatural changes. Here I try to address the generic placement of taxa in Wendling et al.'s (2011) Rapunculus 2 clade.

MATERIALS AND METHODS

Herbarium specimens of all taxa were examined (see acknowledgements for list). All taxa in this paper have been seen in the field except *Campanula aparinoides*. Characters used are almost entirely qualitative and based on examination of herbarium specimens, photographic images, and plants in the field.

TAXONOMIC TREATMENT

Wendling's Rapunculus 2A

This clade contains *Campanula robinsiae*, a Florida annual, *Campanula aparinoides*, an eastern and northcentral perennial, *C. californica* and *C. wilkinsiana,* two perennial California endemics, perennial *Campanula prenanthoides,* which is widespread in California and Oregon, the western annual genera *Githopsis* and *Heterocodon*, and the annual California campanulas. Most of these taxa differ radically from each other (Table 1), except perhaps *C. aparinoides*/*C. californica* and the species pair *C. prenanthoides*/*C. wilkinsiana.*

Campanula robinsiae and *Campanula aparinoides*

Shetler and Morin (1986) suggested that *C. aparinoides* and *C. robinsiae* were distinctive within *Campanula*, each species having unusual seed morphology. Zhou et al. (2012), first pointed out the relationship between *C. robinsiae* and the Asian species *Peracarpa carnosa* Hook. f. & Thomson based on nuclear and plastid DNA. The two species share a mesic to boggy habitat and have small flowers. Yoo et al. (2018) placed *C. aparinoides* and *C. robinsiae* as sister taxa on long branches at the base of the Rapunculus clade, showing them diverging from the rest of the clade and from each other more than 20 m.y.a.

Campanula robinsiae was placed in *Rotantha* (an illegitimate name) with *C. floridana* by Small (1933). It is annual, grows partially submerged in seasonally wet areas, and has terminal flowers that are cleistogamous on submerged branches and chasmogamous on emergent portions, all character states unknown or at least highly unusual in Campanulaceae. The leaves are cauline and linear or narrowly lanceolate, shallowly toothed, and there is no basal rosette (Figure 1). Flowers and capsules are erect, in those of cleistogamous flowers the sepals form a beak over the nearly round capsule (Figure 2), whereas in chasmogamous flowers the sepals remain erect over an oblong capsule that is 3-lobed in cross-section; both forms dehisce by basal pores. The seeds are triangular in cross section and bear conspicuous bulbous papillae on the angles, a state not known in any other Campanulaceae (Shetler and Morin 1986). See Table 1 for comparison of characters. *Peracarpa*, sometimes placed in Peracarpeae Fed., is perennial, has a reduced rosette (Shulkina 1980; Shulkina et al. 2003) and broadly ovate cauline leaves, has terminal and axillary chasmogamous pendulous flowers, capsules dehiscent by irregular tears, and oblong or fusiform seeds (see Barnesky and Lammers 1997 for full description). At least some of the plants have nearly round capsules with small erect or inward-leaning sepals forming a beak (for example, Imperial University 1906, UVMVT158823), or more commonly elongate

elliptic capsules with erect sepals. It grows adjacent to streams or in woodlands. *Campanula robinsiae* is known from only four or five localities, all on the Brooksville Ridge in Hernando and Hillsborough counties (Kunzer et al. 2009) of west-central Florida. This area has diverse topography unusual in peninsular Florida and limestone outcrops unique on the peninsula. *Campanula robinsiae* is treated here as the monospecific genus *Protocodon*.

Figure 1. Holotype of *Protocodon robinsiae* (*Small s.n.*, NY83302).

Figure 2. *Protocodon robinsiae* chasmogamous flower on the left, capsule of cleistogamous flower on the right. Photo: The Rare Plant Conservation Program, Bok Tower Gardens.

PROTOCODON Morin, **gen. nov.**

Type species *Protocodon robinsiae* (Small) Morin

Diagnosis: *Protocodon* is similar to *Peracarpa* in its round capsules; it differs from *Peracarpa* and all other Campanulaceae in the combination of annual habit, linear or narrowly lanceolate cauline leaves, cleistogamous flowers producing nearly round capsules, the sepals forming a beak in fruit, chasmogamous flowers producing straight-sided capsules with erect sepals, seeds triangular in cross-section bearing bulbous projections on the angles, and partially submerged habit.

Etymology: *Proto*, first, *codon*, bell, referring to the phylogenetic placement of this genus, which may have been related to the first Campanuloideae in North America, since it is basal to the rest of the superclade containing the other North American campanuloids.

Species 1, United States, Florida, Brooksville Ridge in Hernando and Highland counties (Figure 8).

Protocodon robinsiae (Small) Morin, **comb. nov**. *Campanula robinsiae* Small, Torreya 26: 35–36. 1926. *Rotantha robinsiae* (Small) Small, *nom. illeg*. Man. S.E. Fl. [Small] 1289. 1933. **Lectotype (**designated here): **Florida**. Packet labeled "Chinsegut Hill," April 1924, *J.K. Small s.n. (*NY 83305!). This sheet has two transparent envelopes on it, one labeled from Chinsegut Hill, Fla., containing a slightly more complete plant, and one from Brooksville, both dated April 1924 in Small's hand. There are multiple plants on the sheet and in a fragment packet. Small stated that the type was at NY. Other collections at NY by Small are from 1931.

Campanula aparinoides (Figs. 3, 4, 5, Table 1) is perennial and grows in seasonally wet areas, sometimes partially submerged. Like *C. californica* it clambers over adjacent vegetation and has retrorse hairs. It has elliptic to linear leaves distributed evenly along the stem. The hypanthium is turbinate, the capsule becoming globose or urceolate, the corolla is bowl-shaped with lobes distinct for about 75% of length, and the capsule is globose or urceolate with basal pores. The stamen filaments are unusual in being densely papillate on both surfaces of the dilated portion, a feature not reported for other Campanuloideae. *Campanula aparinoides* has seeds triangular in cross-section, although not as angular as *Protocodon robinsiae*. *Campanula aparinoides* seeds are unlike any *Campanula* reported to date, with an isodiametric surface pattern, the large surface cells separated by thin radial walls with small holes in them (Shetler & Morin 1986), although *C. olympica* Boiss. may be similar (Akcin 2009). *Campanula aparinoides* is widespread in eastern and north-central North America (Fig. 8); it also occurs in a few localities in Finland and Denmark, where it is introduced. *Campanula aparinoides* is placed here in a new genus, *Palustricodon*.

PALUSTRICODON Morin, **gen. nov**

Type species, *Palustricodon aparinoides* (Pursh) Morin

Diagnosis: *Palustricodon* is similar to *Eastwoodiella* in habit and habitat and presence of retrorse hairs, but differs in being much-branched distally and in having open, bowl-shaped corollas with lobes distinct about 75% the length, capsules ovoid to nearly spherical; seeds generally triangular but without distinct angles in cross-section. It is similar to *Protocodon* in habit and habitat but differs in being perennial and having only chasmogamous flowers.

Etymology: *Palustris*, marsh, and *codon*, bell, alluding to the marsh habitat of this genus.

Species 1, central and eastern North America (Fig. 8).

Palustricodon aparinoides (Pursh) Morin, **comb. nov.** *Campanula aparinoides* Pursh, Fl. Amer. Sept. 1: 159. 1814 [1813]. **Lectotype** (designated here): Southern Expedition of 1806. *F. Pursh s.n.* (PH 908560, Herbarium of Benjamin Smith Barton, image seen). Barbara Cochrane annotated this specimen as the lectotype in 1983 but did not publish the designation.

Palustricodon aparinoides var. grandiflorus (Holz.) Morin, **comb. nov**. *Campanula aparinoides* var. *grandiflora* Holz., Bull. Geol. Nat. Hist. Surv. 9: 566. 1896. **TYPE: USA. Minnesota**. Vermillion, 14 Jul 1891, *J. H. Sandberg 506* (holotype: US 68144, image seen).

Holzinger published identifications of collections housed at US made in Minnesota by Sandberg, according to Holzinger's introduction to the paper. Duplicates of Sandberg's herbarium were purchased and given to the Geological and Natural History Survey of Minnesota. There is no duplicate of *Sandberg 506* at MIN. The specimen at US seems to be the only specimen seen by Holzinger and is the holotype.

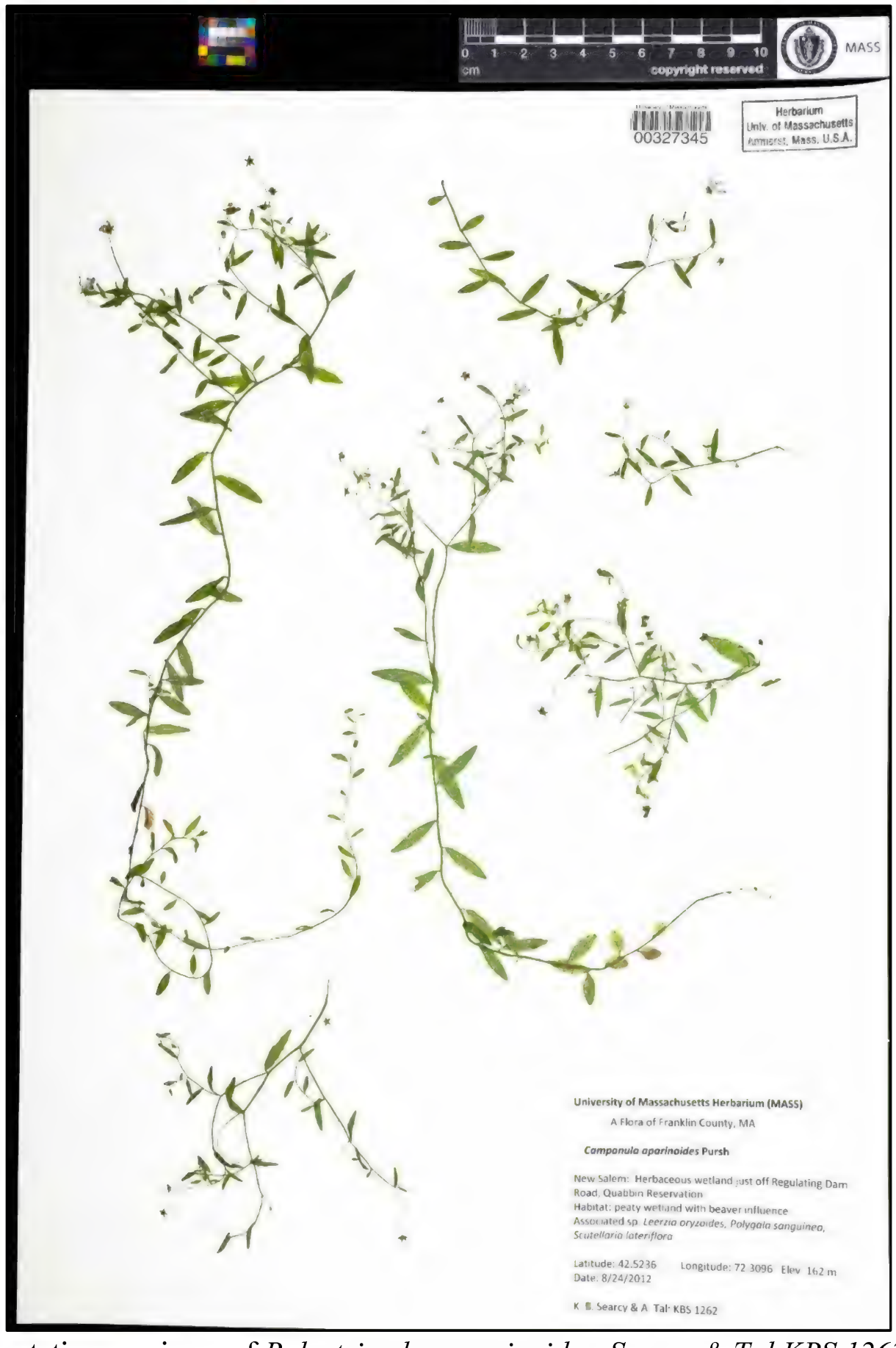

Figure 3. Representative specimen of *Palustricodon aparinoides, Searcy & Tal KBS 1262* (MASS).

Figure 4. *Palustricodon aparinoides*. Photo K. Morse.

Figure 5. *Palustricodon aparinoides* capsule. Photo K. Morse.

Campanula californica

Neither Wendling et al. (2011) nor Yoo et al. (2018) included *Campanula californica* in their analysis, but Crowl (2016) placed *C. californica* (Figs. 6, 7) with the other western North American taxa in the equivalent of Wendling et al.'s Rapunculus 2A clade. *Campanula californica* is a perennial, weak-stemmed plant with elliptic leaves evenly distributed along the stems. The stems and leaves bear fine, retrorse, acicular hairs unusual in Campanuloideae and clamber over adjacent vegetation. *Campanula californica* has a turbinate hypanthium more rounded at base than *Palustricodon*. The corolla is campanulate with lobes that are distinct about half the length, the capsule is hemispheric with somewhat parallel sides, somewhat 3-lobed in cross section. *Campanula californica* grows in very wet areas or in standing water. Both *C. californica* and *P. aparinoides* have seeds with very deep, wide surface cells, perhaps making them buoyant (Shetler & Morin 1986). *Campanula californica* is endemic to coastal California from Santa Cruz County north to northern Mendocino County. Although *C. californica* and *P. aparinoides* are similar in habit and habitat, with buoyant seeds and retrorse hairs, they are not directly related phylogenetically according to molecular studies (Crowl et al. 2016), and their hypanthium and capsule shape and corolla shape are quite different. *Campanula californica* is placed in the monotypic genus *Eastwoodiella*.

Figure 6. *Eastwoodiella californica,* Mendocino County. Photo N. Morin.

Figure 7. Representative specimen of *Eastwoodiella californica, Chambers 5095A* (SRP).

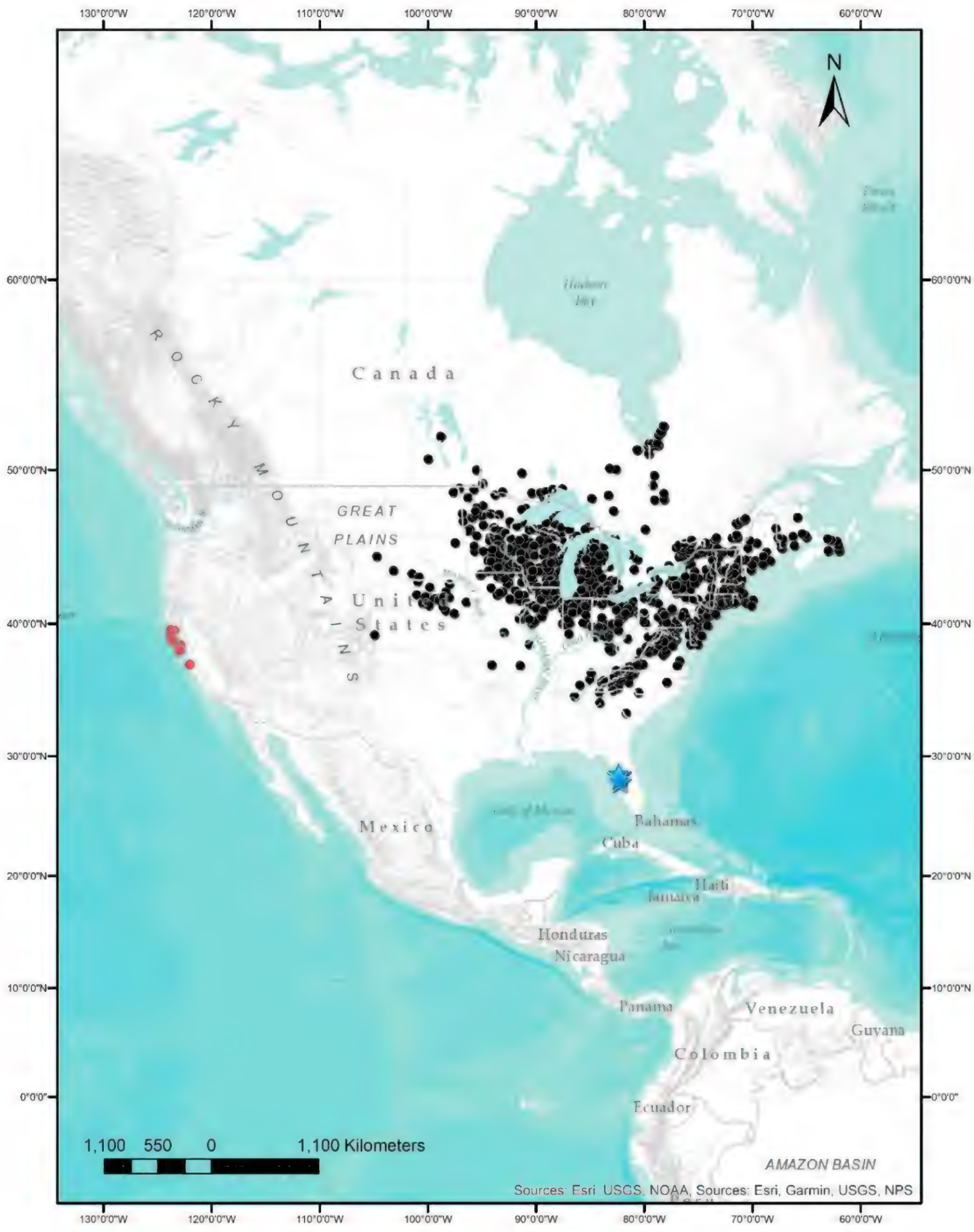

Figure 8. Distribution of *Palustricodon, Eastwoodiella,* and *Protocodon*. Blue stars, *Protocodon robinsiae*, locations based on herbarium specimens in USF. Black circles, *Palustricodon aparinoides*, U.S. distribution showing county presence based on records in Consortium of Northeast Herbaria 2020, Consortium of Pacific Northwest Herbaria 2020, SEINet 2020, and USDA, NRCS 2020; Canadian distribution based on records with coordinates from Consortium of Northeast Herbaria 2020 and Consortium of Pacific Northwest Herbaria 2020. Red circles, *Eastwoodiella californica* (Consortium of California Herbaria 2020).

EASTWOODIELLA Morin, **gen. nov.**

Type species, *Eastwoodiella californica* (Kellogg) Morin

Diagnosis: *Eastwoodiella* is similar to *Palustricodon* in habit and habitat and presence of retrorse hairs; it differs in having a campanulate corolla with lobes distinct about 50% the length, capsules rounded at base with parallel sides, and seeds terete in cross-section. It is similar to *Protocodon* in habit and habitat but differs in being perennial and having only chasmogamous flowers.

Etymology: The genus is named for Alice Eastwood, 1859–1953, revered botanist who was instrumental in developing the herbarium at the California Academy of Sciences and saving many of the type specimens from the 1906 earthquake and fire in San Francisco. She was one of the most prolific plant collectors in California and collected and studied many of the species of California Campanuloideae.

Eastwoodiella californica (Kellogg) Morin, **comb. nov**. *Wahlenbergia californica* Kellogg, Proc. Calif. Acad. Sci. 2:158. 1863. *Campanula californica* (Kellogg) A. Heller, Muhlenbergia 1(3): 46. 1904. **Lectotype** (designated here): Illustration: Fig. 49, based on "a plant brought from the coast range at some point north of San Francisco." No specimen of this taxon collected in 1863 or earlier is extant at CAS. The material seen by Kellogg was presumably lost in the 1906 fire.

Campanula linnaeifolia A. Gray, Proc. Amer. Acad. Arts 7: 366. 1868. **TYPE: California**. Mendocino Co.: Swamps at Noyo, 1866, *Bolander 6571 bis*. (holotype: GH348401! isotypes: BM 901938; CAS 32399!; F 68734!; K 814513!; NY 232342!; PH 908326!; US 3222961!; YU 002081, YU 064154).

Campanula angustiflora, C. exigua, C. griffinii, C. sharsmithiae

Three of the four species of annual California *Campanula* are placed by Crowl et al. (2016) in the equivalent of Wendling et al.'s (2011) Rapunculus 2A clade, in a subclade sister to *Protocodon* and *Palustricodon*. This clade also includes the well-defined annual genera *Heterocodon* and *Githopsis* and perennial *Campanula prenanthoides* and *Campanula wilkinsiana* (the last two treated in the next section).

Fewer than 10% of the species of *Campanula* worldwide are annuals and most of these are in the Mediterranean region (Contandriopoulos 1984). All are in clades very distant from the California taxa (Crowl et al. 2014) and most have been placed in genera other than *Campanula*, e.g., *Annuae* Boiss. and *Roucela* Dumort. for twelve species in the *C. drabifolia* group; *Brachycodon* Fed. [= *Brachycodonia* Fed. ex Kolak.] for *Campanula fastigiata* Duf. ex A.DC, or as subgenera of *Campanula*, e.g., subg. *Megalocalyx* Damboldt, with twelve species in the *C. dichotoma* L. group, and subg. *Sicyocodon* (Feer) Damboldt.

The four annual California species have oblong, turbinate, or rhomboid hypanthia, the capsule dehiscing by medial pores (Morin 1980), setting them apart from the annual genera *Githopsis* (flowers chasmogamous, obconic capsule dehiscent by a hole left when the style falls off) and *Heterocodon* (flowers mostly cleistogamous, capsule broadly obconic or cylindric, dehiscing by basal pores), which also are in Wendling et al.'s (2011) Rapunculus 2A clade. See Table 1 for a comparison of characters.

The species of annual California campanulas are far more similar to each other than they are to any other Campanuloideae species, but they differ from each other in some significant ways. Most North American Campanuloideae have pollen that is 5- to 6-porate, the pores equatorial (Chapman 1966). *Campanula exigua, C. griffinii*, and *C. sharsmithiae* have pantoporate pollen (as do *Eastwoodiella californica* and *Campanulastrum americanum*), whereas most Campanuloideae pollen has 3–4 equatorial pores (Nowicke et al. 1992). *Campanula angustiflora* has 4–6 zonoporate pollen

(Nowicke et al. 1992). The chromosome number of $2n = 34$, found in *C. exigua, C. griffinii*, and *C. sharsmithiae* (Morin 1980), is the most common number in *Campanula* sensu lato, but it is unusual in annual campanulas, for which only $2n = 20$, 24, 28, or 32 had been reported (Gadella 1964; Fedorov & Kovanda 1976; Contandriopoulos 1984). *Campanula angustiflora*, with $2n = 30$, is particularly unusual (Morin 1980) because this count has been reported only for *C. glomerata* L. (including *C. farinosa* (Roch.) Andrz. Ex Bess.) and *C. michauxioides* Boiss. (Gadella 1964), neither of which have any relationship with the California species. *Peracarpa* also has $2n = 30$ as well as $2n = 28$ (Barnesky & Lammers 1997).

Campanula exigua (Fig. 9, 10), *C. griffinii* (Fig. 11), *C. sharsmithiae* (Fig. 12) and *C. angustiflora* (Fig. 13) are placed here in the new genus *Ravenella.*

RAVENELLA Morin, **gen. nov**.

Type species, *Ravenella exigua* (Rattan) Morin.

Diagnosis: *Ravenella* is similar to *Githopsis* in being annual, having divaricately sympodial branching, and occupying xeric habitats. It differs from *Githopsis* and other Campanuloideae having the combination of an oblong, turbinate, or rhomboid hypanthium with dark ribs and pale inter-rib areas, dehiscing by medial pores, and having pantoporate or irregularly 4—6 zonoporate pollen.

Etymology: The genus is named in honor of Peter H. Raven, in recognition of his contributions to our knowledge of the flora of California and his unstinting advocacy for plants of the world and their study.

Species 4, endemic to the California floristic province (Fig. 14).

Ravenella exigua (Rattan) Morin, **comb. nov**. *Campanula exigua* Rattan, Bot. Gaz. (Crawfordsville) 11: 339. 1886. **LECTOTYPE** (designated here): **California**. Contra Costa Co.: Summit of Mt. Diablo, 14 Jun 1886, *V. Rattan s.n.* (JEPS 2508! Fig. 9; isolectotypes: F 372593!, GH 33006!, K 814510!).

Morin (1986) discussed reasoning for considering this JEPS specimen as the type but did not specifically designate it as the lectotype. An additional sheet at JEPS, *Rattan s.n.* June 1886, is probably also part of the type collection. Rattan mentioned two collections, his own from summit of Monte Diablo, 14 June 1886, and a collection by Mrs. Curran, 3 July, on Tamalpais "in full fruit and a larger and coarser form." The Curran specimen is *Ravenella angustiflora*, which accounts for Rattan's reference to the "calyx-lobes … connivant after flowering." Eastwood (1898) in her publication of *Campanula angustiflora* mentioned a collection as *C. angustiflora* by Mrs. Brandegee (= M.K. Curran) made 5 July 1886 from Mt. Tamalpais (see below).

Ravenella angustiflora (Eastw.) Morin, **comb. nov**. *Campanula angustiflora* Eastw., Proc. Calif. Acad. Sci. ser. 3, 1: 132–133. 1898. **LECTOTYPE** (designated here): **California**. Marin Co.: Mt. Tamalpais, 5 Jul 1886, *M.K. Curran s.n.* (CAS131! [image CAS32395!], labeled "holotype" in an unknown hand with an explanatory label by N. F. Bracelin, 1935; isolectotype: US 342449).

CAS 54678! (image CAS32396), annotated as holotype by me in 1980, contains two plants thought to have been remounted from the original CAS131 based on a label hand-written by J.T. Howell that suggested these had been rescued from the 1906 San Francisco fire. The specimen bears two collection labels, one with "*Campanula exigua* Rattan" over which is written "*brandegei* Eastwood sp. nov." collected Summit of Tamalpais 5 July 1886, M.*K.C.* The second bearing "*Campanula angustiflora* Eastw. Mt. Tamalpais, Marin Co. Calif. Coll. Mrs. *K. Curran*, July 5, 1886." Since CAS 131 does exist, however, with no suggestion of material having been removed, it should be the lectotype.

Ravenella griffinii (Morin) Morin, **comb. nov**. *Campanula griffinii* Morin, Madroño 27: 160. 1980. *Campanula angustiflora* Eastwood var. *exilis* J.T. Howell, Leafl. W. Bot. 2: 101. 1938. **TYPE: California**. San Benito Co.: the Pinnacles, 19 May 1937, *Howell 12938* (holotype: CAS 254819!; isotypes: GH 33007!, RSA 2264!, US 1765657!).

Ravenella sharsmithiae (Morin) Morin, **comb. nov.** *Campanula sharsmithiae* Morin, Madroño 27:159. 1980. **TYPE: California**. Stanislaus Co.: Red Mountains, 27 km (17 mi) above mouth of Arroyo del Puerto, Mt. Hamilton Range, 420 m, rocky, almost barren talus slope, associated with *Clarkia breweri*, 19 May 1935, *C.W. and H.K. Sharsmith 3144* (holotype: UC 571938!; isotypes: CAS 4008!; GH 33016!).

Figure 9. *Ravenella exigua*. Photo ©Neal Kramer.

Figure 10. Holotype of *Ravenella exigua* (*Rattan s.n.*, JEPS 2508).

Figure 11. *Ravenella griffinii*. Photo T. Gosliner.

Figure 12. *Ravenella sharsmithiae*. Photo A. Schusteff.

Figure 13. *Ravenella angustiflora.* Photo D. Greenberger.

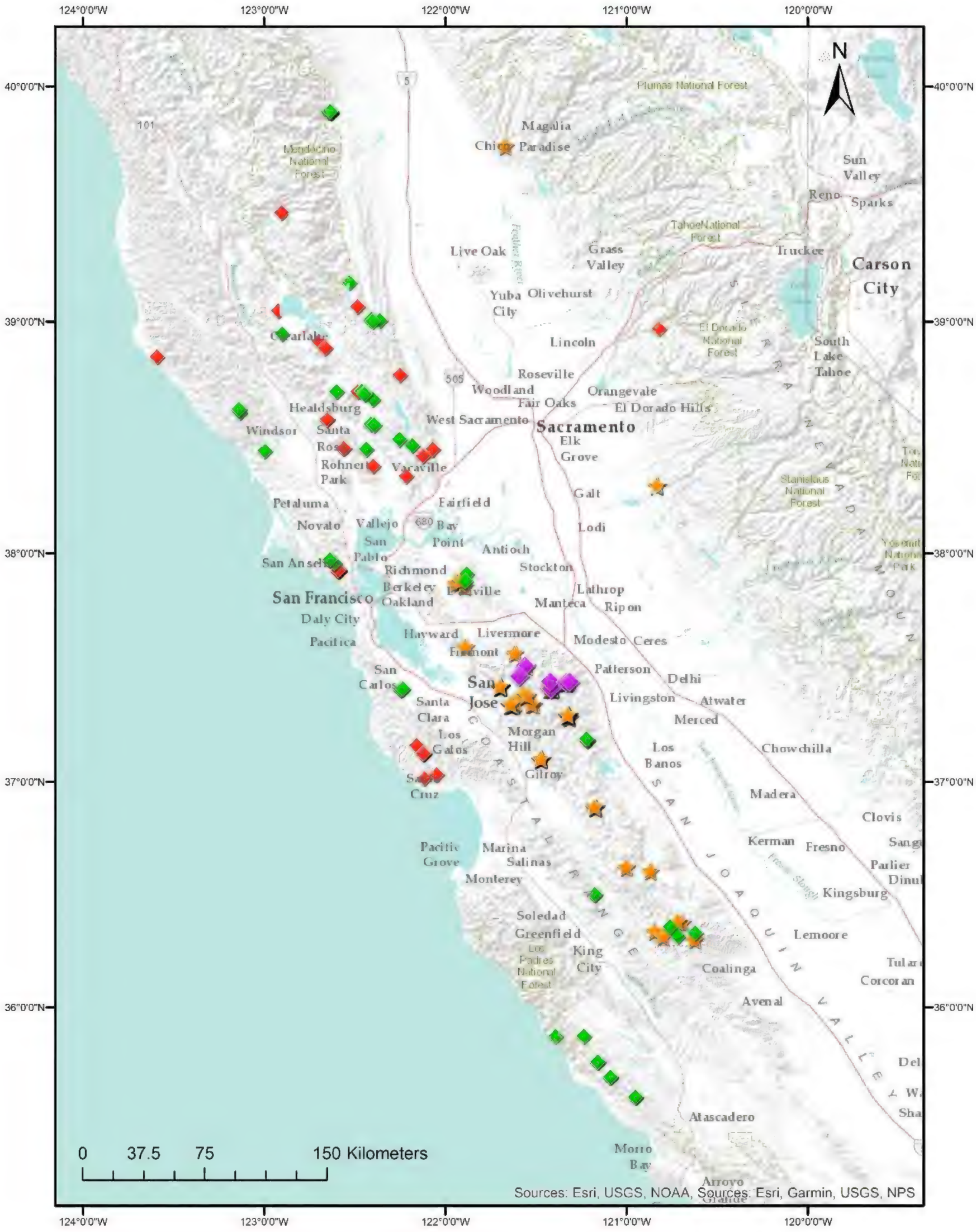

Figure 14. Distribution of *Ravenella. Ravenella griffinii,* green diamonds, *R. angustiflora,* red diamonds; *R. exigua*, orange stars; *R. sharsmithiae* purple diamonds. Consortium of California Herbaria (2020).

Campanula prenanthoides* and *Campanula wilkinsiana

McVaugh (1944) transferred *Campanula prenanthoides* to *Asyneuma* Griseb. & Schenk. He did not say explicitly which characters he thought *C. prenanthoides* shared with *Asyneuma*, but he

pointed out that *Asyneuma* was distinguished from *Campanula* by its deeply divided corolla with tardily separating lobes, and from *Phyteuma* L. by a narrowly paniculate rather than capitate or spicate inflorescence. Damboldt (1968) defined *Asyneuma* as species having corolla lobes connate less than ¼ their length and/or the capsule opening with medial or apical pores. *Campanula prenanthoides* does superficially resemble *Asyneuma,* and in the past I have followed McVaugh in keeping it as *Asyneuma* (Morin 2012), based on its having sulcate stems, flowers sometimes in condensed short shoots, the corolla deeply divided, and the style long-exserted, character states found in various species of *Asyneuma*. In looking more closely at *Asyneuma*, however, I find clear differences. In *Asyneuma* the corolla is divided clear to the base, with the lobes rotate, whereas in *C. prenanthoides* the corolla is divided (66--)75 (--90)%, the lobes are erect distal to the tube and then flare out or reflex. In *Asyneuma* the dilated filament bases are large, often pigmented, and form a structure around the base of the style, the undilated portion immediately distal to this is also stiff and erect; in *C. prenanthoides* the filament bases are dilated but do not form a definite structure, and the rest of the filament is lax. Both *Asyneuma* and *C. prenanthoides* have long-exserted styles; in *Asyneuma*, the papillae are in a clearly defined distal zone, whereas in *C. prenanthoides* the papillae become increasingly less dense proximally. *Campanula prenanthoides* (Figs. 18, 19) has oblong to nearly round capsules (in longitudinal section) that are 3-lobed in cross-section and cordate at base, whereas most *Asyneuma* species have capsules that are obconical and terete in cross-section. *Asyneuma argutum* Bornm., *A. japonicum* (Miq.) Briq., and *A. amplexicaule* (Willd.) Hand.-Mazz. have hemispherical capsules somewhat cordate at base, but none of these species seems to belong in *Asyneuma,* judging from their position in recent phylogenies, and they are not closely related to *C. prenanthoides* (Crowl et al. 2016; Jones et al. 2017). *Campanula prenanthoides* does not belong in either *Campanula* or *Asyneuma*.

Yoo et al. (2018), placed *Campanula wilkinsiana* (Figs. 16, 17) in the equivalent of Wendling et al.'s Rapunculus 2A. Wendling et al. (2011) and Yoo et al. (2018) show *C. wilkinsiana* as sister to *C. prenanthoides*. *Campanula wilkinsiana* grows near standing or flowing water, has a woody caudex and thin rhizomes. Stems and leaves are generally glabrous, and leaves are densely arranged at the base of the stem, then evenly distributed distally. Its corolla lobes are not as deeply cut, and not as narrow as in *C. prenanthoides*, the style is exserted but not as far, the hypanthium is ribbed but more obconic than *C. prenanthoides*. *Campanula wilkinsiana* is known from only two clusters of populations on Mt. Shasta, in northern California. Margins of distal leaves on *Campanula wilkinsiana* have one or two pairs of sharp teeth that extend from the margin rather than being incised in it, and one pair near the apex, a character state also found in *Ravenella exigua*. It may be that *C. wilkinsiana* is the result of ancient hybridization or other gene flow among *Eastwoodiella californica, C. prenanthoides*, and/or *Ravenella exigua*. *Campanula prenanthoides* and *C. wilkinsiana* are here placed in a new genus, as follows.

SMITHIASTRUM Morin, **gen. nov**.

Type species, *Smithiastrum prenanthoides* (Durand) Morin

Diagnosis: *Smithiastrum* is similar to *Eastwoodiella* and *Palustricodon* in being a slender perennial, lacking a basal rosette, and having cauline leaves sessile or subsessile. It differs from them and other Campanuloideae in the combination of having the flowers terminal or axillary, pedicellate or nearly sessile, sometimes both in one inflorescence, solitary or in interrupted spikelike clusters, sometimes somewhat capitate, or inflorescence paniculate with longer pedicels, the hypanthium widely cylindrical or obconic, base squared and somewhat cordate, sepals very narrowly lanceolate, corolla with petals distinct in distal 66--90% of length, tube cylindrical or somewhat funnelform, sometimes slightly constricted below lobes, lobes linear or narrowly lanceolate, spreading to recurved; capsule hemispherical, oblong, or obconic, dehiscing by pores central or apical in center of the area between each lobe or broad rib.

Etymology: *Smithiastrum* is named in honor of James Payne Smith, Jr., emeritus faculty member in the Biology Department of Humboldt State University; a pioneer in plant conservation, authority on uses of plants especially by native peoples and on the toxicity of plants. The name also alludes to the star-shaped quality of the flowers.

Species 2, coniferous forests, California in the western Sierra Nevada, Cascade Range, Klamath Range, North Coast Range, and western Oregon in the Coast and Cascade Ranges (Fig. 15).

Figure 15. Distribution of *Smithiastrum, Poolea, Rotanthella.* Red circles, *Smithiastrum prenanthoides*; yellow stars, *Smithiastrum wilkinsiana* (Consortium of California Herbaria 2020; Consortium of Pacific Northwest Herbaria, 2020). Green diamonds, *Poolea reverchonii* (specimen records from BRIT). Blue triangles, *Rotanthella floridana* (Wunderlin et al. 2020).

Figure 16. *Smithiastrum wilkinsiana*. Photo E. White.

Figure 17. Representative specimen of *Smithiastrum wilkinsiana* (C. Hart Merriam Aug. 1885. US1677682).

Figure 18. Representative specimen of *Smithiastrum prenanthoides* (BLM MD003281).

Figure 19. *Smithiastrum prenanthoides*. Photo S. Matson.

Smithiastrum prenanthoides (Durand) Morin, **comb. nov**. *Campanula prenanthoides* Durand, Pl. Pratten. Calif. 93. June 1855; J. Acad. Nat. Sciences, Philadelphia, ser. 2, 3:93. December 1855. **LECTOTYPE** (designated here)**: California**, Nevada City, *s.d.., Pratten s.n.* (Barcode PH 414!, specimen stamp M1038627) containing Durand's handwritten Latin description and handwritten ticket; *Asyneuma prenanthoides* (Durand) McVaugh.

Smithiastrum wilkinsiana (Greene) Morin, **comb. nov**. *Campanula wilkinsiana* Greene, Pittonia 4:33. 1899. **LECTOTYPE** (designated here): **California**. Head of Squaw Creek, Mt Shasta, Aug 1898, *L. Wilkins s.n.* (US 1677682! image 146789).

Greene mentioned two specimens, both from Squaw Creek, one from August and one from September. The August specimen has good flowers and well-pressed leaves; the September specimen has developing capsules, poorly preserved. The August 1898 specimen is therefore chosen as the lectotype.

Campanula baileyi Eastw., Bull. Torrey Bot. Club 29: 525. 1902. **TYPE: California**. Trinity Co.: Mountains at the head of Canyon Creek, Aug 1899, *V. Bailey s.n.* (holotype: CAS 133).

Campanula reverchonii* and *Campanula floridana

Wendling et al.'s (2011) clade Rapunculus 2B is close but not immediately adjacent to the taxa discussed above. It contains the North American *Triodanis, Campanula reverchonii, Campanula floridana*, and *Campanulastrum americanum* (Table 2), which together are sister to European *Legousia* and more distantly related to *Asyneuma. Popoviocodonia uyemurae* (Kudô) Fed. is sister to the larger clade (Crowl et al. 2016 and Mansion et al. 2012, although Jones et al. 2017 has it as sister to *Campanula uniflora*).

Triodanis is an annual that generally grows in dry areas, often in grassland. It has clusters of chasmogamous and cleistogamous flowers that are sessile in axils of broad, nearly round bracts or narrower, lanceolate bracts, in an unbranched, spikelike inflorescence; the hypanthium and capsule are broadly cylindrical or clavate but not narrow and not or barely narrower below the sepals, corollas are light or mid-blue or lavender, the lobes elliptic to narrowly elliptic, the center paler but not a bright white, sharply defined eye, lobes distinct nearly to base; capsule broadly cylindrical or clavate, pores near the base, central, or near the apex, round, broadly oblong, slit-like, or capsule splitting from top. The Texan *Triodanis coloradoensis* (Buckley) McVaugh diverges from these patterns and is more similar to *Legousia falcata* (Ten.) Fritsch: the central white area of the corolla is slightly more defined than in other *Triodanis*, the hypanthium is longer, much thinner than other *Triodanis* and similar in length and width to *L. falcata*, the flowers terminal on branches from the axils of narrow bracts or sessile in axils, distal ones chasmogamous, proximal ones cleistogamous. *Triodanis leptocarpa* Nieuwl. also has a narrow hypanthium and narrow leaves and bracts, spicate inflorescence, and both chasmogamous and cleistogamous flowers. Of the seven species, Mansion et al. (2012) included *T. coloradoensis*, *T. leptocarpa*, *T. biflora*, and *T. perfoliata*, but without much resolution.

The European genus *Legousia* is a small annual with flowers sessile in axils of moderately narrow bracts in a branched or unbranched inflorescence, all chasmogamous, with corollas that are deep blue-purple, the lobes nearly round or very broadly elliptic, with a sharply delineated white center, the lobes distinct nearly to the base, the hypanthium and capsule cylindrical and very narrow, constricted just below the sepals, pore small, near apex. *Legousia falcata*, which McVaugh (1945) treated in *Triodanis,* supported by Haberle et al.'s analysis (2009), differs in having flowers with broad blue corolla lobes, the central white area less distinctly demarcated, the hypanthium cylindrical but broader than core *Legousia*, the flowers terminal on elongated axillary branches, distal flowers chasmogamous, proximal flowers cleistogamous. Wahlsteen and Tyler (2019) revisited the circumscription of taxa in *Legousia*.

Campanulastrum Small is a tall, coarse annual or biennial, with flowers in spikes composed fascicles of 1—5-flowered cymes in axils of lanceolate bracts, all chasmogamous, with corollas that are pale to bright, light blue or lavender blue, generally with a white central area, the lobes nearly rotate, distinct nearly to the base, lanceolate to deltate-ovate, hypanthium and capsules narrowly obconic, pores near the apex. The style of *Campanulastrum* is very long, declined and upcurved, a character state seen in *Campanula aurita* and *C. versicolor* (Janković et al. 2019).

Campanula reverchonii, a divaricately branching annual (Fig. 20) of xeric habitats, has terminal flowers, all chasmogamous, with narrowly campanulate, light lavender-blue corollas with longitudinal cream-colored areas and a dark purple ring at the base adaxially, the lobes distinct for 50—60% of the length (Fig. 21), differs from any *Campanula, Triodanis,* or *Legousia* in the shape of its narrowly ellipsoid hypanthium and capsule. It resembles *Triodanis* only in the shape of its seeds, which are lenticular, and in the dehiscence of the capsule. In both *T. coloradoensis* and *C. reverchonii* the pore opens from the top down, whereas in all other Campanuloideae in which dehiscence is by pores, the pores open from the bottom up (Shetler 1963; Shetler & Morin 1986).

Campanula floridana is a weak-stemmed, prostrate or clambering perennial of marshes, swamps, and similar wet areas, with flowers terminal, all chasmogamous, hypanthium and capsule obconic, corolla lobes distinct nearly to base, dark purple, linear-lanceolate. The capsule opens by a wide pore initiated near the base that occupies most of the space between the ribs. The seeds have seed coats with large lumina and irregularly shaped foramina in the walls, the surface rugose (Shetler & Morin 1986).

Campanula floridana and *C. reverchonii* cannot be kept as *Campanula*, neither fits into the other genera in this clade, and they do not resemble each other morphologically or in habit. Each is placed in a monotypic genus here.

POOLEA Morin, **gen. nov.**

Type species, *Poolea reverchonii* (A. Gray) Morin, **comb. nov**.

Diagnosis*: Poolea* is similar to *Githopsis, Ravenella,* and *Heterocodon* in being an erect annual with sympodial branching. It is similar to *Githopsis* and *Ravenella* in having narrow bracts and leaves. It differs from these genera in having an inflorescence with long internodes and in the shape of the hypanthium and capsule. It differs from *Triodanis* in having sympodial branching and in lacking cleistogamous flowers. It differs from *Rotanthella* in being annual and erect rather than perennial and clambering or prostrate. *Poolea* differs from these genera and from all other Campanuloideae in the combination of having the hypanthium and capsule ellipsoid with the pores near the apex and the valve opening at the top, curving down.

Etymology: *Poolea* is named in honor of Jackie M. Poole, botanist with the Texas Parks and Wildlife Department for more than thirty years, an effective and passionate advocate for plant conservation, especially of the Texas flora.

Poolea has one species. It is endemic to the Llano Uplift area of the Edwards Plateau, in central Texas (Fig. 15).

Poolea reverchonii (A. Gray) Morin, **comb. nov**. *Campanula reverchonii* A. Gray, Syn. Fl. N. Amer. 2(1): 396. 1886 (as "*Reverchoni*"). **TYPE: Texas**. Llano, 1885, *J. Reverchon s.n.* (holotype: GH [barcode 00348407]).

This specimen has a handwritten label, with "*Campanula reverchoni* n. sp." Gray wrote: "On granitic rocks, House Mountain, Llano and Burnet Co. Reverchon 1885" in the original description. Duplicates of the May 1885 collection under the number 1548 were widely distributed with a printed label headed "Texas Plants" and "*Campanula reverchoni*, Gray n. sp. Clefts of granitic rocks, House Mountain, Llano Co., May [no year given]." (duplicates are at CAS, CM, F, MO-3 sheets, NY-2 sheets, UC, US-2 sheets). It seems probable that Reverchon sent Gray one specimen, the one with the handwritten label, and after receiving the determination from Gray, produced the printed labels, which accompanied the duplicates he distributed. Therefore, the GH specimen is the one Gray would have seen. A sheet at MO (3460223) has an entirely handwritten label that reads "*Campanula reverchoni* Gr, granitic soil, House Mt., Llano (crossed out) Mason Co., May 1884-fr Burnet Co July 1884." A sheet at Kew has a label printed ex herb A. Gray and handwritten "*Campanula reverchoni* n. sp. A. G., Reverchon 1885, Texas" (image K000814507). Reverchon apparently collected this taxon in July 1884, Burnet Co., Texas, also numbered 1548, specimen at Missouri Botanical Garden (image MO 3460224). He may have mentioned this collection to Gray, which would account for the inclusion of Burnet Co. in the original description.

Figure 20. *Poolea reverchonii*. Holotype, *Reverchon s.n.*, 1885 (GH).

Figure 21. *Poolea reverchonii*. Photo C. Chang.

ROTANTHELLA Morin**, nom. nov**., a replacement name for *Rotantha* Small, Man. S.E. Fl. [Small] 1289. 1933, non *Rotantha* Baker, J. Linn. Soc. Bot. 25: 317. 1890.

Type species, *Rotanthella floridana* (S. Wats. ex A. Gray) Morin

Rotanthella is similar to some *Triodanis* in having an obconic hypanthium and capsule and corolla rotate with lobes distinct almost to base. It differs from *Triodanis* in being perennial, prostrate to clambering, lacking cleistogamous flowers, and its aquatic or mesic habitat. It differs from all other Campanuloideae in the combination of perennial habit, prostrate or clambering stems, basal rosette of leaves absent, cauline leaves evenly distributed, hypanthium obconic, corolla rotate or nearly so, petals free to base, capsule obconic to oblong-obconic, opening by oblong pores that occupy most of the space between ribs.

Etymology: Small did not give a reason for his choice of *Rotantha* as the name for this genus. The corollas of *Rotanthella floridana* are markedly rotate and the name may have alluded to that.

Rotanthella has one species, occurring in shallow water and wet ditches throughout most of Florida (Fig. 15), with outlying populations reported from Georgia, North Carolina, and Alabama (no precise localities, not shown on map).

Figure 22. *Rotanthella floridana*. Photo M. Groeneveld.

Figure 23. *Rotanthella floridana*. Photo A. de la Paz.

Figure 24. Representative specimen of *Rotanthella floridana* (*Lakela 25900*, USF).

Rotanthella floridana (S. Wats. ex A. Gray) Morin, **nom. nov**. *Campanula floridana* S. Wats. ex A. Gray, Syn. Fl. N. Amer. 2(1): 13. 1878. *Rotantha floridana* (S. Wats. ex A. Gray) Small, Man. S.E. Fl. [Small] 1289. 1933. **Lectotype** (designated here): "East Florida, coll. Edward Palmer, M.D., 1874, Indian River, *C. floridana* n. sp. S.W." (GH, image GH 68140!).

This sheet appears to have four collections on it, two of which are by A.P. Garber, and the other two, by Palmer and Feay, are cited in the original description by Gray. The Palmer collection is a plant with small, elliptic leaves. It is nearest the label and is the least ambiguous as to collector. It has both a flower and a capsule. The Feay collection is in an envelope. Florida, Pease River, Dr. Feay, GH image GH68140!; K, image K000814514, NY, image NY00232343 (from Chapman Herbarium in the Columbia College Herbarium). Specimens labeled *Campanula calycosa* Torr., n.sp., "East Florida (from Dr. Torrey 1859)", at GH (image HUH1795516) and one labeled "*Campanula calycosa* Torr. & Gr. n. sp., = *floridana* A. Gray 1841" at Kew (image: K000814515) are also *Rotanthella floridana*.

Campanula uniflora

Campanula uniflora, Wendling et al.'s (2011) Rapunculus 2C clade, which is circumarctic and occurs in the high alpine regions of western North America, was, with *Petromarula* Vent. ex R. Hedw., sister to *Asyneuma, Physoplexis,* and *Phyteuma* in Schneeweiss et al. (2013), and in a clade with *Petromarula* and *Asyneuma japonicum* in Yoo et al. (2018). *Campanula uniflora* is unique in having a dark blue hypanthium, the capsule clavate, becoming nearly black, pore near apex. *Campanula uniflora* is not similar in any way to these other genera. Fedorov (1957) assigned *Campanula uniflora* to *Campanula* subsect. *Melanocalyx*, which is elevated to genus here.

MELANOCALYX (Fed.) Morin, **stat. nov.** *Campanula* L. subsect. *Melanocalyx* Fed., Flora S.S.R. XXIV: 467. 1957. **Type species**: *Melanocalyx uniflora* (L.) Morin

Melanocalyx uniflora (L.) Morin, **comb. nov.** *Campanula uniflora* L., Sp. Pl. 1: 231. 1753. **LECTOTYPE**: Herb. Linnaeus No. 221.2 (LINN [digital image!)], Ferrer-Gallego (2019).

Figure 25. Distribution of *Melanocalyx uniflora* (GBIF 2020; Consortium of Pacific Northwest Herbaria 2020; Consortium of Northeastern Herbaria, 2020; SEINet 2020).

Figure 26. Representative specimen of *Melanocalyx uniflora* (*Patterson & Beaty*, August 1882. UVMVT158007).

DISCUSSION

Wendling et al. (2011) suggested that campanuloid ancestors colonized North America at least six times:

1. *Campanula chamissonis*, the Aleutian species of the *Campanula* clade, with an east Asian origin (Yoo et al. 2018).
2. Rapunculus 2A, which, based on Yoo et al. 2018, would have a Eurasian origin through an ancestor shared with *Peracarpa*.
3. Rapunculus 2B, from an introduction of a relative of the Macaronesian/Mediterranean *Legousia* (Jones, 2017).
4. Rapunculus 2C, *Campanula uniflora*, from east Asia (Roquet et al. 2008; Wendling et al. 2011; Yoo et al. 2018).
5. Rapunculus 1A, the "Cordilleran" species, high elevation and alpine taxa.
6. Rapunculus 1B, *Campanula rotundifolia*, also with a European origin.

Earlier authors also had hypothesized multiple introductions less explicitly (e.g., Morin, 1983; Shetler & Morin 1986; Eddie et al. 2003; Haberle et al. 2009; Mansion et al. 2012).

Wendling et al.'s Rapunculus 2A Clade

Phylogenetic analysis of Peracarpeae (Zhou et al. 2012) showed that the eastern Asian monotypic *Peracarpa* constituted a clade with North American *Heterocodon*, *Githopsis*, and three species now in new genera: *Protocodon*, *Ravenella*, and *Smithiastrum*, supporting a Campanuloideae disjunction between Eurasia and North America 16.84 (13.12–20.97) m.y.a. (Zhou et al. 2012). Yoo et al. (2018) suggested this split occurred earlier, more than 30 m.y.a. Yoo et al. (2018) estimated that *Palustricodon*, now widespread in central and eastern North America, separated from *Protocodon*, now limited to a small area in Florida, about 18 m.y.a. *Protocodon* appears to be a relict in the Brooksville Range, which may have remained above sea level during the Pleistocene (James 1961). It exhibits characters that appear again in various other North American taxa, such as occurrence in wet habitats, annual habit, clambering aspect, sympodial branches, leaves evenly distributed on the stem, cleistogamy, and specialized seeds (Table 1).

The *Palustricodon*/*Protocodon* clade is sister to the remaining species in Rapunculus 2A, all western taxa (Yoo et al. 2018). The similarity in habit, habitat, and special features like retrorse hairs shared by *Eastwoodiella* and *Palustricodon* suggests that these two taxa have retained some characters from a common ancestor. *Ravenella*, *Smithiastrum*, *Heterocodon*, and *Githopsis* diverged from *Protocodon*/*Palustricodon* about 22 m.y.a. (Yoo et al. 2018); perennial, woodland *Smithiastrum prenanthoides* split from *Ravenella*/*Heterocodon*/*Githopsis*, all annuals, about 10 m.y.a. (Yoo et al. 2018). *Eastwoodiella,* limited to coastal California, was not included in the more recent studies but is placed in this clade by Mansion et al. (2012) and Crowl et al. (2016); its 3-lobed hypanthium and capsule suggest a relationship with the more widespread *Smithiastrum prenanthoides*. *Ravenella* and *Githopsis* both show the rapid speciation typical of annuals adapted to xeric conditions and specialized soil types in the California Floristic Province (Raven & Axelrod 1978). The presence in *Ravenella* of a chromosome number of $2n = 34$ (Morin 1980) and pantoporate pollen in all but *R. angustiflora*, which has $2n = 30$ and 4–6 zonoporate pollen (Nowicke et al. 1992), suggests there is more complexity in this genus that needs study. *Ravenella* and *Githopsis* have both self-pollinating and outcrossing species (Morin 1980, 1983). *Githopsis tenella*, known from only three populations in Kern and Tulare counties, California, shares the presence of both chasmogamous and cleistogamous flowers and broad bracts (Morin 1983) with the widespread *Heterocodon*, which has predominantly cleistogamous flowers.

Wendling et al.'s Rapunculus 2B clade

Legousia, a European genus of annuals, is sister to the North American taxa in Rapunculus 2B, the separation occurring about 20 m.y.a. (Yoo et al. 2018). *Campanulastrum* is basal to the North American portion of the clade, with *Poolea* sister to *Triodanis* and *Rotanthella.* Except for *Poolea,* these taxa share an obconic or cylindrical hypanthium and capsule and a deeply divided corolla (Table 2). Barnard-Kubow et al. (2015) suggested that the distribution of *Campanulastrum* represented multiple lineages that survived the Last Glacial Maximum in at least three refugia in the Appalachians and on the Atlantic and Gulf Coasts, which subsequently migrated north. *Poolea*, a relict annual limited to the Llano Uplift of central Texas, split from annual *Triodanis* and perennial *Rotanthella* more than 10 m.y.a. (Yoo et al. 2018). The center of diversity of *Triodanis* is in Texas (McVaugh 1945; Haberle et al. 2009): *Triodanis coloradoensis* and *T. texana* McVaugh are limited to central Texas and the remaining five species are more or less widespread, with their distribution including Texas. They all occupy relatively xeric habitats. *Rotanthella*, in contrast, is perennial and occurs in wet habitats. Its position in the clade might argue for inclusion in *Triodanis*, but its distinctive growth form, flower morphology, and habitat suggest it is on a different evolutionary path from *Triodanis*.

Wendling et al.'s Rapunculus 2C clade

The relationships of the arctic-alpine *Melanocalyx uniflora* to other Campanuloideae is unclear. It is placed in a clade with *Petromarula, Phyteuma,* and *Physoplexis* in Wendling et al. (2011). *Melanocalyx* is not similar morphologically to any of these.

Additional considerations

Campanuloideae taxa in North America have been separated from Eurasian relatives for millions of years (Yoo et al. 2018). Within North America, some of them are separated from each other by vast distances and dramatically different topography. Over geologic time their populations will have expanded and contracted, so even geographically distant species, or their ancestors, may have grown together at one time or another. The western species in Rapunculus 2 often grow sympatrically with each other or in close approximation in various combinations, although usually occupying different microhabitats. In the east, distributions of *Campanulastrum* and *Triodanis* overlap, as do the *Triodanis* and *Poolea* distributions. Some taxa in Wendling et al.'s (2011) Rapunculus 1 clade (the "cordilleran" species and *C. divaricata*, as well as *C. rotundifolia*) are sympatric with Rapunculus 2 species. Flower morphology is distinctive in some of these species, but the general pollination mechanism is similar in all of them and there is no reason to suppose that cross-pollination cannot occur. The possibility of historic gene flow should be kept in mind when untangling relationships in the remaining North American campanuloids.

CONCLUSION

These new North American genera reflect habitat similarities, geographic distribution, morphological similarities, and genetic affinities as expressed in phylogenetic analyses. They differ morphologically from each other and from other Campanuloideae at least as much as, or more than, most other genera in the subfamily. Retaining them in *Campanula* obscures their relationships and makes it difficult to portray phytogeographic patterns. Recognizing them as new, well-defined genera will facilitate consideration of evolutionary patterns in the family and on the continent.

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Table 1. Wendling et al.'s (2011) Rapunculus Clade 2A, part 1. **Annuals**.

	Protocodon	*Ravenella*	*Heterocodon*	*Githopsis*
Duration	annual	annual	annual	annual
Height/length	3---26 cm	2---25 cm	1.5--30 cm	1--40 cm
Habit	clambering	erect	erect	erect
Roots	fibrous	slender taproot	slender taproot	slender taproot
Leaf distribution	evenly distributed	below inflorescence	evenly distributed (bracts leaflike)	below inflorescence
Cauline leaf shape	elliptic to narrowly lanceolate	linear-subulate to oblong-ovate	round to ovate	oblong to ovate
Leaf blade length	5--10 mm	2--11 mm	2--10 mm	3.5--20 mm
Inflorescence*	sympodial/leader replaced (flower offset)	sympodial/ leader replaced or dichotomous	sympodial/ leader replaced (flower offset)	sympodial/leader replaced (flower offset) or dichotomous
Flowers/axis	many	many	many	many
Cleistogamous flowers	present	absent	present	absent (present)
Hypanthium shape	spheric (cl), cylindrical cordate (ch)	oblong, turbinate, or rhomboid	obconic to cylindric	cylindric or obconic
Corolla length	4--5 mm	2.2--18 mm	3--5 mm	2.5--24 mm
Petals %distinct	85--95%	30--60%	30--40%	20--80%
Corolla shape	campanulate	funnelform-campanulate or cylindric	cylindric-campanulate	cylindric, funnelform, or campanulate
Corolla lobe shape	narrowly elliptic	deltate	triangular or ovate-triangular	elliptic to deltate
Style exsertion**	included	included	included	included or exserted
Style curved	straight	straight	straight	straight
Stigma	25--33%	10--30%	25%	10--15%

Table 1. Wendling et al.'s (2011) Rapunculus Clade 2A, part 1. **Annuals, continued**.

	Protocodon	*Ravenella*	*Heterocodon*	*Githopsis*
Capsule shape	globose or urceolate	oblong, oblong-obconic, obovoid to spheric	urceolate or cylindrical	cylindric, funnelform, or campanulate
Hypanthium ribs	absent	narrow, dark, interspersed with pale inter-rib areas	raised, flat/sulcate inter-rib areas	prominent, adjacent (inter-rib areas absent or narrow)
Sepal aspect	forming a beak	erect or forming a beak	rotate	erect to spreading
Capsule pore position	basal	central	basal	base of style
Capsule pore extent	small	small	small	n/a
Seeds	triangular in x-section, angles sharp, conspicuous protruberances on angles	fusiform, round in x-section, striate or smooth	elliptical, terete in x-section, smooth	fusiform, terete in x-section, striate
Habitat	riparian	xeric	mesic	xeric
Geographic distribution	Florida: Brooksville Ridge	central California	Rocky Mountains west	western states

*Sympodial (flower offset): New branch from axil of leaf/bract straight and continuous with main axis, flower offset opposite leaf/bract. Dichotomous: new branch from axil of leaf/bract appears to fork, giving dichotomous appearance.

**Style exsertion depends on both shape of corolla (rotate or open cup vs. narrow tube) and relative length of style.

Table 1. Wendling et al.'s (2011) Rapunculus Clade 2A, part 2. **Perennials**.

	Palustricodon	*Eastwoodiella*	*Smithiastrum prenanthoides*	*Smithiastrum wilkinsiana*
Duration	perennial	perennial	perennial	perennial
Height/length	10--300 cm	10--30 cm	20--80 cm	5--30 cm
Habit	clambering	clambering	erect or spreading	erect
Roots	slender rhizomes	slender rhizomes	from woody caudex	from woody caudex
Leaf distribution	evenly distributed	evenly distributed	evenly distributed	concentrated proximally
Cauline leaf shape	elliptic to linear	elliptic	ovate to lanceolate	ovate-lanceolate to lance-oblong
Leaf blade length	6--45 mm	10--20 mm	10--60 mm	12--20 mm
Inflorescence*	sympodial/ appearing dichotomous	monopodial becoming dichotomous/ leader replaced	monopodial	monopodial
Flowers/axis	many	single	many	single
Cleistogamous flowers	absent	absent	absent	absent
Hypanthium shape	obconic becoming semi-globose	hemispheric	cylindric, base cordate	obconic to cylindric
Corolla length	5--15 mm	8--15 mm	7--14 mm	12--15 mm
Petals %distinct	75--80%	50--70%	66--90%	50%
Corolla shape	bowl-shaped	campanulate to funnelform	tube cylindrical	funnelform
Corolla lobe shape	deltate	oblong-deltate	linear to linear-lanceolate	narrowly lanceolate
Style exsertion**	exposed	included	long-exserted	slightly exserted
Style curved	straight	straight	straight or curved	straight
Stigma	33%	15%	10%	15--30%
Capsule shape	globose or urceolate	cup-shaped, 3-lobed in cross section	cylindric to hemispheric, 3-lobed in cross section	narrowly obconic to oblong, terete

Table 1. Wendling et al.'s (2011) Rapunculus Clade 2A, part 2. **Perennials, continued**.

	Palustricodon	*Eastwoodiella*	*Smithiastrum prenanthoides*	*Smithiastrum wilkinsiana*
Hypanthium ribs	obscure	grouped alternating with inter-rib areas	grouped, prominent	dark
Sepal aspect	erect	spreading	rotate or reflexed	ascending
Capsule pore position	basal	basal	central	apical
Capsule pore extent	small or capsule wall disintegrates	small	medium	small
Seeds	± triangular in x-section, angles rounded, surface with ±hexagonal plates	elliptical to obovate, ovate in x-section, interrupted striate	oblong, ovate-flattened in x-section, surface striate	not known
Habitat	riparian	riparian	mesic	mesic, high elevation
Geographic distribution	c, e N. Amer.	California coast	California, Oregon	California: Mt. Shasta

*Sympodial (flower offset): New branch from axil of leaf/bract straight and continuous with main axis, flower offset opposite leaf/bract. Dichotomous: new branch from axil of leaf/bract appears to fork, giving dichotomous appearance.

**Style exsertion depends on both shape of corolla (rotate or open cup vs. narrow tube) and relative length of style.

Table 2. Wendling et al.'s (2011) Rapunculus Clade 2B and 2C.

	Rapunculus 2B				**Rapunculus 2C**
	Campanulastrum	***Triodanis***	***Poolea***	***Rotanthella***	***Melanocalyx***
Duration	annual/ biennial	annual	annual	perennial	perennial
Height/length	(20--) 210 cm	5--100 cm	5--35 cm	15--40 cm	4--10(--15) cm
Habit	erect	erect	erect	clambering/ prostrate	erect
Branching	monopodial	monopodial	sympodial dichotomous	sympodial dichotomous	unbranched from woody, branched caudex
Leaf distribution	evenly distributed	evenly distributed	below infl.	evenly distributed	mostly basal
Leaf shape	ovate to broadly lanceolate	lanceolate to suborbiculate	spatulate	broadly ovate to elliptic	broadly ovate to spathulate
Leaf blade length	60--120 mm	5--35 (-70) mm	5--15 mm	8--40 mm	7--30 mm
Inflorescence	flowers in axillary fascicles	flowers axillary, 1 or in fascicles	flowers terminal	flowers terminal	flowers terminal
Flowers/axis	many	many	many	many	one
Cleistogamous flowers	absent	present	absent	absent	absent
Hypanthium shape	obconic	obconic	ellipsoid	ovate-turbinate	oblong ellipsoid
Corolla length or diam.	20--30 mm diam.	10--24 mm diam.	12--16 mm long	14--18 mm diam.	6--12 mm long
Petals %distinct	80--90%	70--85%	55--65%	95%	33--55%
Corolla shape	rotate	rotate	funnelform to campanulate	± rotate	campanulate to funnelform
Corolla lobe shape	deltate-ovate	elliptic, ovate, or oblong	elliptic to ovate-lanceolate	narrowly oblong-lanceolate	narrowly triangular
Style exsertion	long-exserted	exserted	included	exserted	included
Style curved	sigmoidally curved	straight	straight	straight	straight
Stigma lobes	5--10%	15--17%	15%	10%	10%

Table 2. Wendling et al.'s (2011) Rapunculus Clade 2B and 2C, continued.

	Wendling et al.'s (2011) Rapunculus 2B				Rapunculus 2C
	Campanulastrum	*Triodanis*	*Poolea*	*Rotanthella*	*Melanocalyx*
Capsule shape	obconic	cylindrical to obovoid	ellipsoid to obovoid	hemispheric to obovoid	clavate (dark blue to black)
Hypanthium/ capsule ribs	faint	capsule sulcate	faint	ribs thin, grouped	ribs thin, spaced
Sepal aspect	spreading	spreading	forming a beak	spreading	erect
Capsule pore position	apical	apical, central, below center (*T. coloradoensis* top down)	apical, opening top down	most of inter-rib area	apical
Capsule pore extent	medium	small to extensive	most of inter-rib	most of inter-rib	medium
Seeds	oblong, lenticular, pebbled	smooth or muricate; *T. texana* quadrangular, basket weave surface	broadly elliptical/ roundish, lenticular, striate	broadly elliptical to quadrangular, terete-ovate, rugose	oblong, terete, striate
Habitat	mesic	xeric to mesic	xeric	aquatic	alpine
Geographic distribution	central/eastern North America	throughout North America	Llano uplift, Texas	Florida & adjacent states	circumboreal

*Sympodial (flower offset): New branch from axil of leaf/bract straight and continuous with main axis, flower offset opposite leaf/bract. Dichotomous: new branch from axil of leaf/bract appears to fork, giving dichotomous appearance.

**Style exsertion depends on both shape of corolla (rotate or open cup vs. narrow tube) and relative length of style.

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DESMODIUM URARIOIDES (FABACEAE: PAPILIONOIDEAE), UN NUEVO REGISTRO PARA LA FLORA VASCULAR DE EL SALVADOR

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ABSTRACT

The occurrence of *Desmodium urarioides* is recorded in two localities of El Salvador after its identification and a bibliographic review. It previously was known only from Mexico. Habitat, distribution, collection data, and in situ photographs are presented.

RESUMEN

Se registra la ocurrencia de *Desmodium urarioides* en dos localidades de El Salvador, anteriormente conocida solo de México, después de su identificación y revisión bibliográfica exhaustiva. Se presenta, hábitat, distribución, datos de colecta y fotografías *in situ*. Por otra parte, con estos datos se amplía su ámbito de distribución local y regional.

Se presenta el primer reporte de *Desmodium urarioides* (S.F. Blake) Schub. & McVaugh para El Salvador, al mismo tiempo se amplía su ámbito de distribución.

En El Salvador, se reportan un total de 23 especies de *Desmodium* registrados en los herbarios LAGU del Jardín Botánico La Laguna y MHES del Museo de Historia Natural de El Salvador, incluyendo *D. urarioides*. La información para esta especie es bastante escasa, la única descripción encontrada es en por McVaugh (Flora Novo-Galiciana 5: 494. 1987).

El material depositado en LAGU fue determinado por L. Torres Colín en 05-2017 [vía e-mail]; además, en 2018 se revisó el material salvadoreño depositado en MEXU (*Linares & Martínez 2158*), determinado también por L. Torres Colín. Con el material identificado, se realizó una investigación bibliográfica exhaustiva y en los sitios web Tropicos.org y Jstor Global Plants, en ninguno se encontró algún reporte para El Salvador.

Material examinado. **EL SALVADOR. Depto. Santa Ana**. Mpio. Candelaria de la Frontera: Entre Cerro Peña del Cuervo y Cerro El Yupe, 14°8’30”N 89°40’9” W, 1300 m, 9 dic 1994, *Linares & Martínez 2158* (EAP, MEXU); El Mosco, entre el Cerro Peña del Cuervo y el Cerro El Yupe, ca. 3 km al SSO de Tierra Blanca y 3 km al NO de Candelaria de la Frontera, 14.133° -89.683°, 1120 m, 28 nov 1999, *Linares 4606* (MEXU); Mpio. Metapán, P.N. Montecristo, El Guachipilín, Calle a Los Planes, cerca de entrada a Torre Guachipilín, 14°23’13.9”N 89°23’30.6”W, 1451 m, 01 feb 2017, *Galán & Molina 4050* (LAGU, MEXU, MO) y 4 feb 2020, *Galán, Perdido & Matute 5252* (LAGU, MEXU, MO).

Hábitat. Bosque de robles y vegetación de encinar perturbado de *Quercus peduncularis*, *Quercus* sp., y *Pinus oocarpa*; además en un predio baldío dentro de bosque tropical semideciduo mixto submontano, bien drenado.

Distribución. De acuerdo a la base de registros en Tropicos (2020), su distribución se restringe a México; sin embargo, aún no se ha enviado el material más reciente de El Salvador a MEXU y MO.

Para este trabajo, se toma de referencia el mapa de distribución de IBUNAM el cual incluye a El Salvador con el material de J.L. Linares depositado en MEXU (Fig. 1).

En base al material de referencia local, para la distribución nacional se presentan dos localidades en el departamento de Santa Ana (Fig. 2).

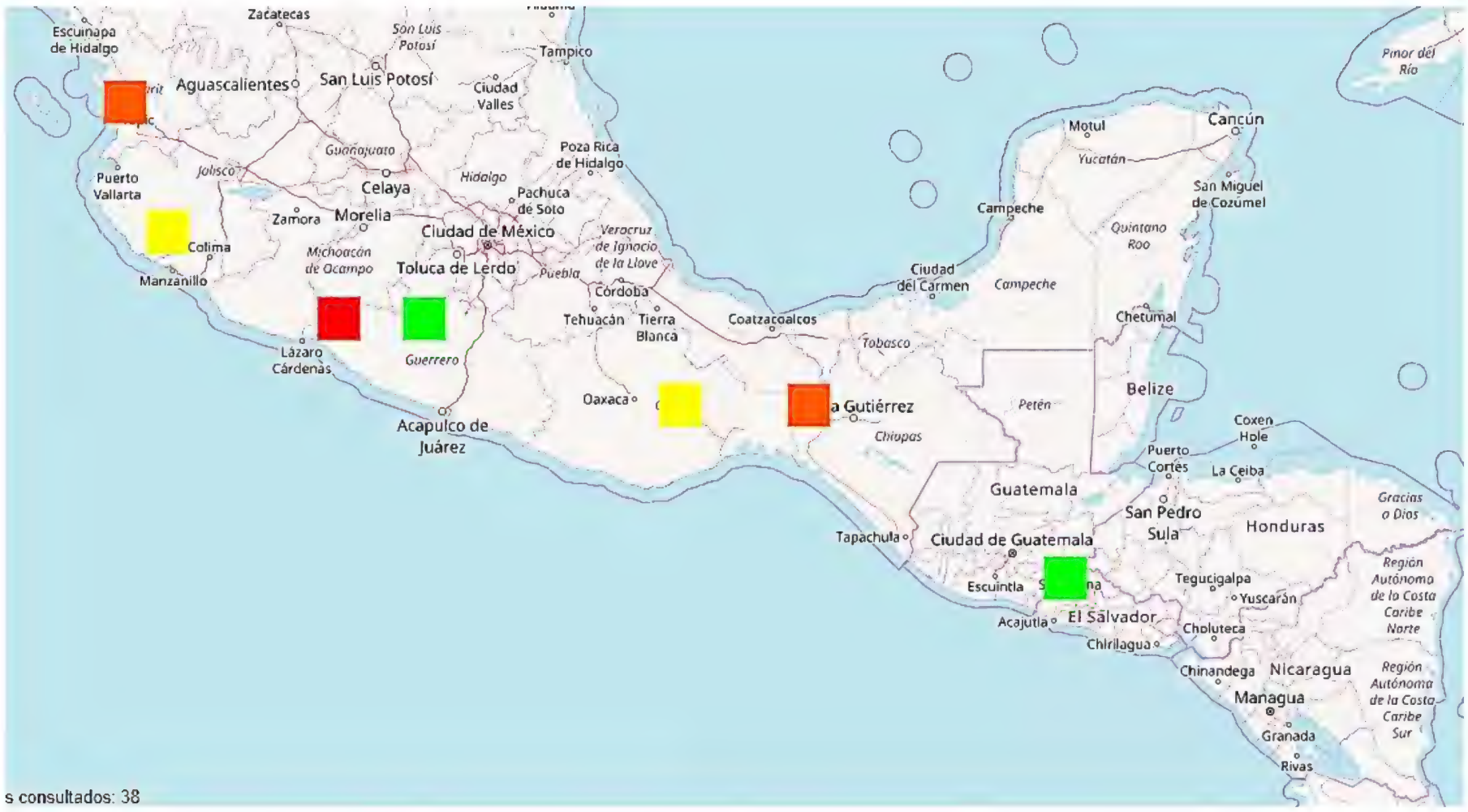

Figura 1. Distribución conocida *de Desmodium urarioides.* Fuente: Departamento de Botánica, Instituto de Biología (IBUNAM).

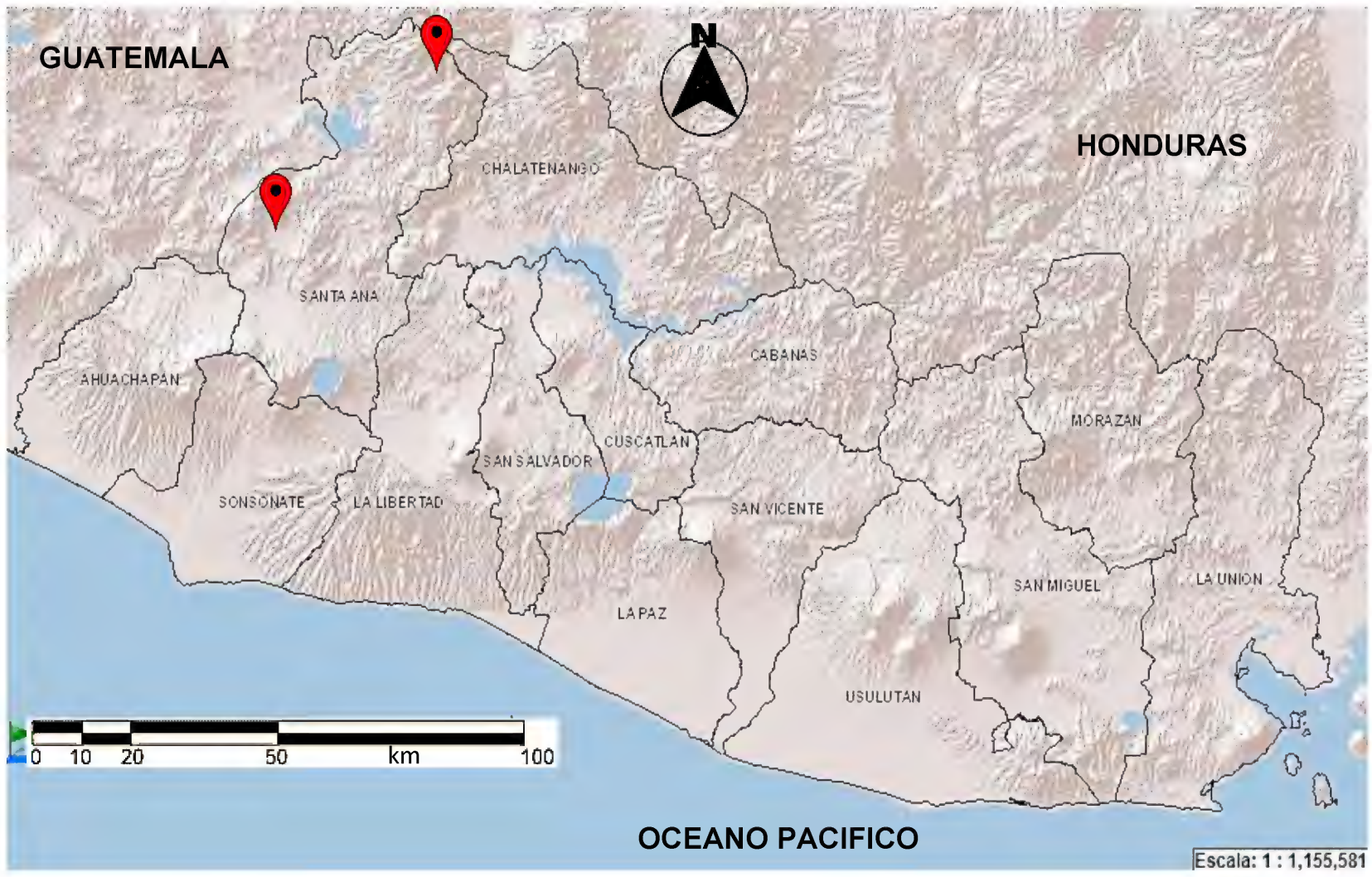

Figura 2. Distribución de *Desmodium urarioides* en El Salvador. Mapa base: MARN, 2020.

Figura 3. *Desmodium urarioides.* A. Flor. B. Follaje.

Figura 4. *Desmodium. urarioides.* A. Inflorescencia con flores y fruto. B. Hábito y hábitat.

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Leticia Torres Colin de herbario MEXU por apoyar en la identificación; al personal del herbario MEXU de la UNAM por permitir el acceso a sus colecciones en junio de 2018, a Jenny Menjívar de herbario MHES por el acceso a sus colecciones en 2019.

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DIEZ NUEVOS REGISTROS PARA LA FLORA VASCULAR DE EL SALVADOR

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ABSTRACT

Ten species are reported for the first time for flora of El Salvador, including *Centrosema pascuorum*, *Cissus cacuminis*, *Davilla kunthii*, *Indigofera costaricensis*, *Kearnemalvastrum subtriflorum*, *Manfreda pubescens*, *Nicotiana plumbaginifolia*, *Paullinia turbacensis*, *Stevia connata*, and *Trifolium repens*, a non-native (naturalized) species. Photographs, herbarium citations, scans of specimens, and a distribution map of all species are presented.

RESUMEN

Se reportan un total de diez especies nuevas para la flora de El Salvador, entre ellas *Centrosema pascuorum*, *Cissus cacuminis*, *Davilla kunthii*, *Indigofera costaricensis*, *Kearnemalvastrum subtriflorum*, *Manfreda pubescens*, *Nicotiana plumbaginifolia*, *Paullinia turbacensis*, *Stevia connata*, y *Trifolium repens*, una especie no nativa (naturalizada). Se presentan scan de algunos ejemplares de herbario, fotografías, material revisado en herbarios y un mapa de distribución nacional de todas las especies.

Se realizó una revisión exhaustiva de especímenes en los herbarios LAGU del Jardín Botánico La Laguna y MHES del Museo de Historia Natural de El Salvador, consulta en la literatura local y regional, anterior y más reciente, así como en bases de datos digitales entre ellos Tropicos de Missouri Botanical Garden, en los cuales no se encontraron registros o mención sobre las especies referidas en este artículo.

Algunas especies cuentan con registros de veinte años o más, pero habían sido identificadas erróneamente bajo otro taxón como el caso de *Manfreda pubescens*, la cual posteriormente fue determinada por el autor y confirmada por A. García-Mendoza en 2019; otra especie permaneció en el taxón de familia Malvaceae y fue determinada por L.J. Dorr en 2016 como *Kearnemalvastrum subtriflorum* con un duplicado enviado a US (fide Smithsonian National Museum of Natural History 2017); *Nicotiana plumbaginifolia* fue colectada en 1999 y posteriormente en 2014, sin embargo no existen registros para El Salvador en la literatura revisada; por otra parte, *Centrosema pascuorum* fue colectada en 2003, pero fue determinada hasta 2015 por J.E. Jiménez; *Trifolium repens* es una especie no nativa-naturalizada en todo el continente y a pesar que existe un registro histórico de Molina en 1963 depositado en US, no se encontró ninguna publicación que haga referencia a su ocurrencia en El Salvador; mientras que el resto de las especies corresponden a colectas realizadas en los últimos cuatro años por el personal del herbario del Jardín Botánico La Laguna y determinadas recientemente.

En total se reportan diez especies nuevas para la flora del país, distribuidas en seis departamentos, siendo Santa Ana el que presenta la mayor parte con siete especies, de las cuales seis se encuentran en el Parque Nacional Montecristo al norte en el municipio de Metapán.

ASPARAGACEAE

Manfreda pubescens (Regel et Ortgies) Verhoek ex Piña, Cact. Suc. Mex. 31: 16. 1986.
Agave pubescens Regel et Ortgies, Gartenflora 23: 227. 1874. *Agave brachystachya* var. *pubescens* (Regel et Ortgies) A. Terracc.

MATERIAL EXAMINADO:

AHUACHAPÁN: P.N. El Imposible, San Benito, al S de Monte Hermoso, 13°49'N 89°56'W, 9 jul 1994 (flr), *Chinchilla s.n.* (ISB00527) (B, LAGU); P.N. El Imposible, San Benito, al pie de la Vereda Los Escobos, 13°49'N 89°56'W, 650 m, 11 sep 1997 (frt), *Sandoval 1681* (B, EAP, ITIC, LAGU, MO). **SANTA ANA**: Mpio. Metapán, Crío. El Rosario, Cerro La Experiencia, Bosque Pino-Roble, 14°21'34"N 89°22'54"W, 1080 m, 12 sep 2013, *Cerén, Menjívar, Baños & Mendoza 3076* (MHES); Mpio. Metapán, P.N. Montecristo, Buena Vista, Quebrada de Vidal, 14°22'25.28''N 89°24'2.18''W, 1174 m, 10 ago 2016 (frt), *Martínez 34 (JBL07849)* (LAGU).

Figure 1. *Manfreda pubescens*. Ejemplar en herbario (LAGU).

ASTERACEAE

Stevia connata Lag., Gen. Sp. Pl. 27. 1816.
Stevia viminea Schrad. ex DC.

MATERIAL EXAMINADO:

SANTA ANA: Mpio. Metapán, P.N. Montecristo, Las Experiencias, Bosque siempreverde estacional aciculifoliado de tierras bajas bien drenado (MARN, 2011), 14°22'6.6"N 89°23'0.3"W, 1342 m, 9 oct 2019 (flr), *Galán & Molina 5165* (LAGU, MEXU, MO).

Figure 2 A, B. *Stevia connata*. **A.** Ejemplar en herbario (LAGU). **B**. Detalle de inflorescencias.

Figure 2C. *Stevia connata*. Hojas.

DILLENIACEAE

Davilla kunthii A. St.-Hil, Pl. Usuel. Bras. sub t. 22 (1824 [1825]).
Davilla aspera (Aubl.) Benoist. *Tigarea aspera* Aubl.

MATERIAL EXAMINADO:

MORAZÁN: Mpio. San Fernando, Ctón. Azacualpa, Crío. Platanares, sendero a Cascada El Chorrerón, Área abierta, orilla de sendero, 13°57'47.01''N 88°13'45.92''W, 733 m, 13 feb 2019 (frt), *Galán et al. 4949* (LAGU, MO).

Figure 3. *Davilla kunthii*. Ejemplar en herbario (LAGU).

FABACEAE

Centrosema pascuorum Mart. ex Benth.
Bradburya pascuorum (Mart. ex Benth.) Kuntze

MATERIAL EXAMINADO:

MORAZÁN: Mpio. Arambala, Cantón Cumaro, A.P. Río Sapo, Camino a Piedra X, 13°55'N 88°60'W, 686 m, 15 oct 2003 (flr, frt), *Carballo & Monterrosa 976* (LAGU).

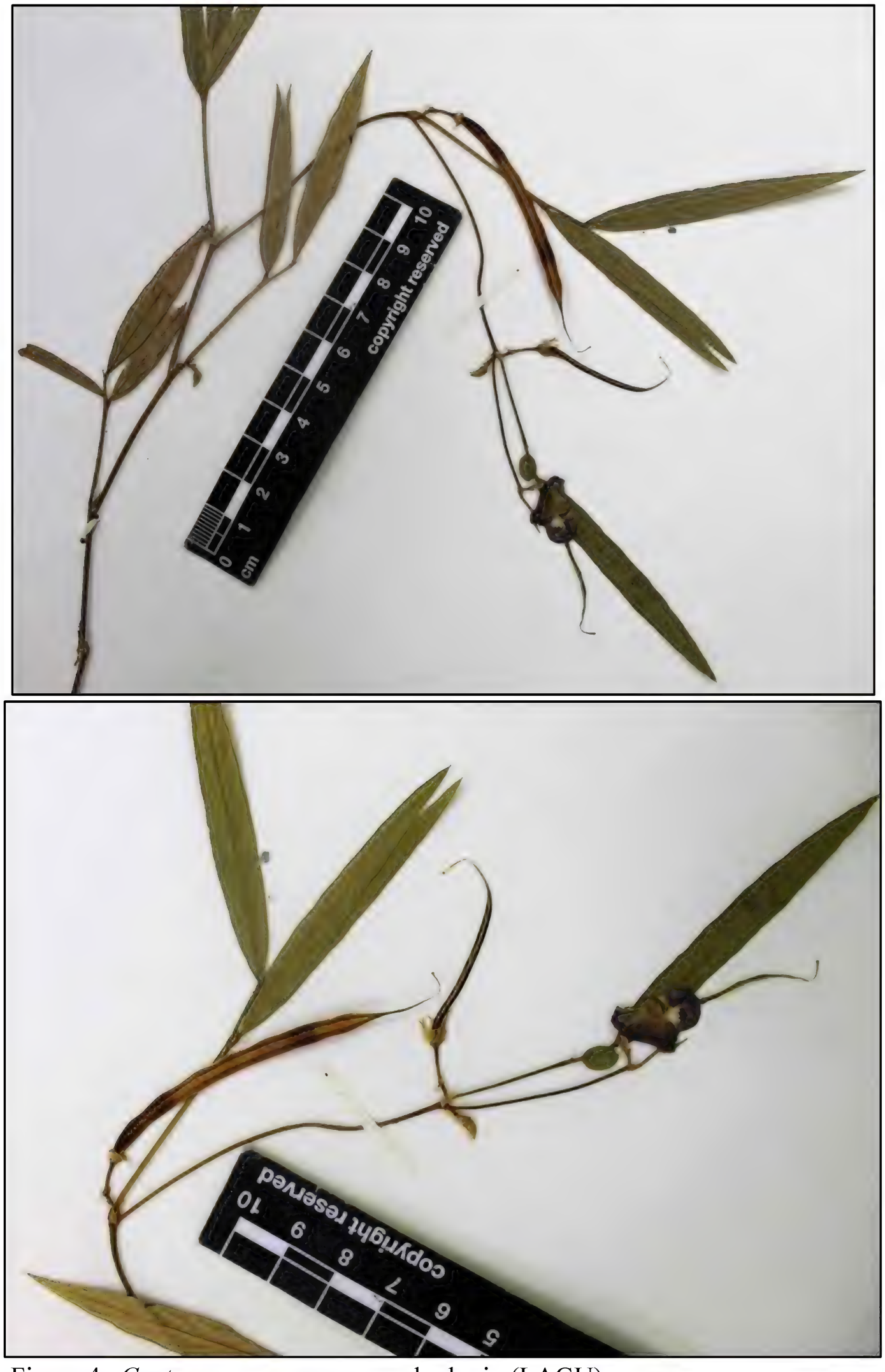

Figure 4. *Centrosema pascuorum* en herbario (LAGU).

Indigofera costaricensis Benth, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1853: 5. 1854. *Indigofera thibaudiana* sensu Lievens (1992, pro parte), non DC.

MATERIAL EXAMINADO:

SANTA ANA: Mpio. Metapán, P.N. Montecristo, El Terrero, Bosque tropical semideciduo mixto montano inferior, bien drenado, 14°22'39.4''N 89°23'34.7''W 1306 m, 8 nov 2016 (flr, frt), *Galán & Martínez 386* (B, K, LAGU, MO); P.N. Montecristo, El Astillero, Bosque tropical semideciduo mixto montano inferior, bien drenado, 14°22'42.8''N 89°23'38.1''W 1392 m, 2 feb 2017 (frt) *Galán, & Orellana 4059* (B, LAGU, MEXU, MO).

CHALATENANGO: Mpio. San Ignacio, Ctón. Río Chiquito, Bosque de Conífera, 14°21'31.7"N 89°7'55.3"W, 1979 m, 17 nov 2017 (flr), *Hernández s.n.* (MHES, MO).

Figure 5. *Indigofera costaricensis*. **A**. Material en herbario (LAGU). **B**. Planta *in situ.*

Trifolium repens L., Sp. Pl. 767. 1753.

MATERIAL EXAMINADO:

SANTA ANA: En el bosque denso y nebuloso de Montaña de Montecristo, 2300 m, 23 may 1963 (flr), *Molina 12624* (US); Mpio. Metapán, P.N. Montecristo, Los Planes, alrededores de Auditorium, Área abierta, 14°23'55.2"N 89°21'36.7"W, 1851 m, 7 mar 2019 (flr), *Galán 5017* (LAGU, MEXU, MO); San José Ingenio, P.N. Montecristo, alrededores del anfiteatro de Los Planes, Vegetación predominante de *Cupressus* y área de cultivo de flores, 14°23'58.3"N 89°21'39.8"W, 1863 m, 9 may 2019, (flr), *Rodríguez 7321* (LAGU).

Figure 6. *Trifolium repens.* A. *In situ.* B. Ejemplar de herbario.

MALVACEAE

Kearnemalvastrum subtriflorum (Lag.) D.M. Bates, Brittonia 19: 232. 1967.
Malva subtriflora Lag., Elench. pl./Gen. sp. pl. 21. 1816; *Malvastrum mexicanum* (S. Schauer) Hemsl.; *M. ribifolium* (Schltdl.) Hemsl.

MATERIAL EXAMINADO:

SANTA ANA: Mpio. Chalchuapa, Cantón El Paste, Volcán Chingo, sendero principal al cráter, bosque tropical semideciduo latifoliado montano inferior, bien drenado, 13°7'3.67"N 89°43'22.03"W, 1607 m, 23 oct 2012 (flr), *Rodríguez & Marroquín 3677* (LAGU, US).

Figure 7. *Kearnemalvastrum subtriflorum*. Ejemplar en herbario (LAGU).

SAPINDACEAE

Paullinia turbacensis Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 5: 114. 1821.
Paullinia wetmorei Standl.

MATERIAL EXAMINADO:

SANTA ANA: Metapán, San José Ingenio, P.N. Montecristo, calle a Caja de Agua, Bosque tropical semideciduo mixto submontano, bien drenado, 14°21'50"N 89°23'52.9"W, 908 m, 11 jun 2015 (frt), *Rodríguez, López & Magaña 5308* (B, LAGU, US); P.N. Montecristo, Caja de Agua hacia San José Ingenio, frente a Casa de Anselmo, Bosque tropical semideciduo mixto submontano, bien drenado, 14°21'54.8"N 89°23'49"W, 945 m, 27 jul 2016 (flr, frt), *Galán & Martínez 3727* (LAGU, MO, US).

Figure 8. *Paullinia turbacensis*. Material en herbario (LAGU), con frutos.

SOLANACEAE

Nicotiana plumbaginifolia Viv., Elenchus Plantarum Horti Botanici 26, pl. 1. 1802.
Nicotiana cavanillesii Dunal; *Nicotiana crispa* Cav. 1802

MATERIAL EXAMINADO:

LA LIBERTAD: Mpio. Colón, Ctón. Las Angosturas, Carretera a Santa Ana, Proyecto Urbanización Montemar Fase III, Sistema agropecuario / Cafetal,13°44'17''N 89°20'58''W, 587 m, 27 abr 2014 (flr, frt), *Galán, Álvarez, & Bonilla 2864* (BM, LAGU, MEXU, NY).

SAN MIGUEL: Laguna El Jocotal, Creciendo a orilla de la laguna en vegetación secundaria, 11 jun1999 (flr, frt), *Villacorta & Echeverría 2378* (B, LAGU, MO).

Figure 9. *Nicotiana plumbaginifolia*. **A.** Ejemplar en herbario (LAGU). **B**. Planta in situ, detalle de flores y frutos.

VITACEAE

Cissus cacuminis Standl., Field Mus. Nat. Hist., Bot. Ser. 17: 375. 1938.

MATERIAL EXAMINADO:

SANTA ANA: Mpio. Metapán, P.N. Montecristo, alrededores de Cárcava #4, 14°23'21''N 89°23'17.5''W, 1535 m, 8 de mayo de 2019 (flr), *Galán & Molina 5085* (B, LAGU, MO, US).

Figure 10. *Cissus cacumini.* **A**. Ejemplar en herbario (LAGU).

Figure 10. *Cissus cacumini.* **B**. Inflorescencia *in situ.*

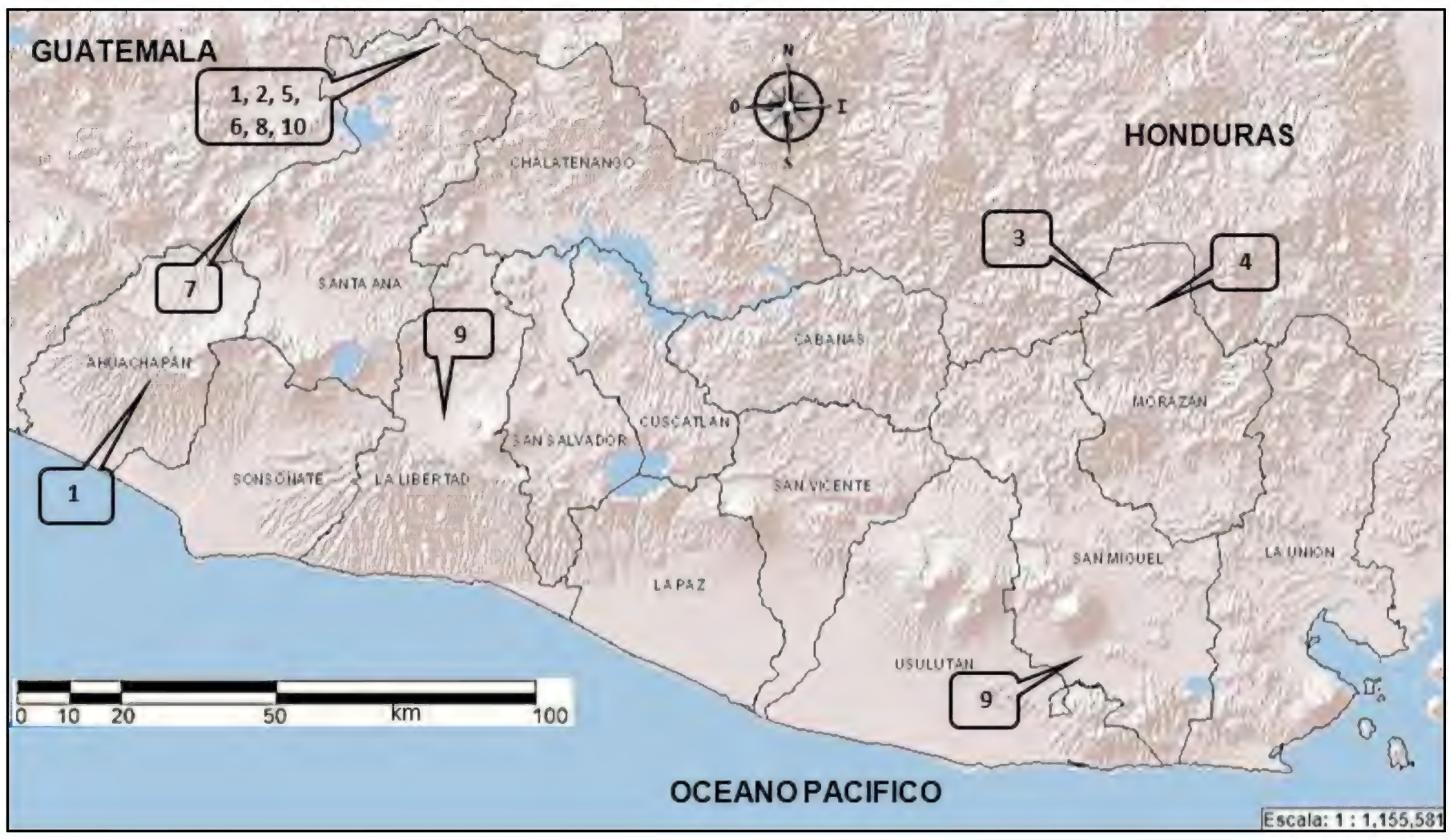

Figure 11. Distribución de las especies.

1 Manfreda pubescens
2 Stevia connata
3 Davilla kunthii
4 Centrosema pascuorum
5 Indigofera costaricensis
6 Trifolium repens
7 Kearnemalvastrum subtriflorum
8 Paullinia turbacensis
9 Nicotiana plumbaginifolia
10 Cissus cacuminis

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A Jenny Menjívar de Herbario MHES por la accesibilidad y consulta de sus colecciones, a Abisaí García-Mendoza por revisión de material de *Manfreda pubescens*, a Lilian Ferrufino por apoyar en búsqueda de material en herbario TEFH.

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Nesom, G.L. 2020. Geography of *Erigeron abajoensis* (Asteraceae). Phytoneuron 2020-52: 1–18. Published 19 August 2020. ISSN 2153 733X

GEOGRAPHY OF *ERIGERON ABAJOENSIS* (ASTERACEAE)

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ABSTRACT

Erigeron abajoensis occurs from southeastern Utah into northwestern New Mexico and immediately adjacent Arizona. It does not overlap in distribution with *E. caespitosus*, which reaches its southernmost extension in northern Utah and northern Colorado. A map shows the distribution of *E. abajoensis* and a series of geographically representative herbarium specimens illustrates its morphology.

Erigeron abajoensis Cronq. was characterized by Nesom (2006, p. 283) as a "segregate of *E. caespitosus* Nutt., separated from the latter only by its strigose (versus hirsute) stems and leaves and greater tendency for 1-nerved leaves," who also said that (p. 283) it might be considered a "regional variant" of *E. caespitosus*. The protologue (Cronquist 1947, p. 169) noted that "*E. abajoensis* is related to *E. caespitosus*, from which it differs in the appressed cauline pubescence, single-nerved leaves, and slightly longer style-appendages." Despite their similarity, the nodding buds and reflexing ray corollas of *E. abajoensis* (vs. erect buds and coiling ray corollas in *E. caespitosus*) suggest that they are not so closely related. Instead, *E. abajoensis* appears to belong with species of sect. *Stenactis* (lectotype *E. pumilus*; also including *E. clokeyi*, *E. concinnus*, *E. maguirei*, *E. vetensis*, and others), characterized as taprooted perennials with 1-nerved leaves, relatively unreduced stem leaves, 1–few heads per stem, nodding buds, and reflexing rays (Nesom 2008). Among these, *E. maguirei* Cronq., from Emery and Wayne counties, Utah, is closest in morphology to *E. abajoensis*.

Erigeron caespitosus has been included in the floras of Arizona and New Mexico (e.g., Cronquist 1994; Nesom 2006; Welsh et al. 2015) but it ranges from Alaska through western Canada, into Idaho, Montana, and North Dakota, reaching its southern extensions in northern Utah and northern Colorado. It does not overlap in range with *E. abajoensis*, which occurs from southeastern Utah into northwestern New Mexico and adjacent Arizona (Fig. 1). Cronquist (1994) noted an Arizona collection of *E. caespitosus* from San Francisco Mt. (Coconino Co.; probably *Jones s.n.*, POM, 6 Aug 1884, from Flagstaff, which he cited in 1947) — I have not seen this collection but it almost certainly is some other species. The only collections of *E. abajoensis* I have seen from Arizona are these: Apache Co.: N end of Tunitcha Mts. near Luka-Chukai Mountains, volcanic rock, near Roof Butte, 2800 m, 4 Jul 1936, *Goodman & Payson 2915* (NY, Fig. 11); Navajo Nation, Carrizo Mts, Teec Nos Pos Canyon, granite cliffs, permanent stream, pinyon-juniper and edge of ponderosa pine, 6668–6808 ft, 15 Sep 2001, *Reeves 10503* (NAVA); Chuska Mts, Sonsela Buttes, SW rim of east butte, E of tall rock outcrop, in cracks of basalt, ponderosa pine, gambel oak, 8480 ft, 20 Aug 1991, *Hevron 1385a* (NAVA).

Despite a consistency in morphology, the distribution of *Erigeron abajoensis* is discontinuous, particularly in New Mexico, where it occurs abundantly in both the Beautiful Mountain area of San Juan County (Figs. 8, 9) and the Mt. Taylor area of Cibola County (Figs. 12–14). Those around Mt. Taylor grow at 10,650–11,400 feet while those around Beautiful Mountain grow at 8700–9200 feet, suggesting that the two systems are physiologically differentiated. The plants in Catron County (Fig. 10) were collected at 6800 feet. In Utah, the elevational range is 6800–11,350 feet.

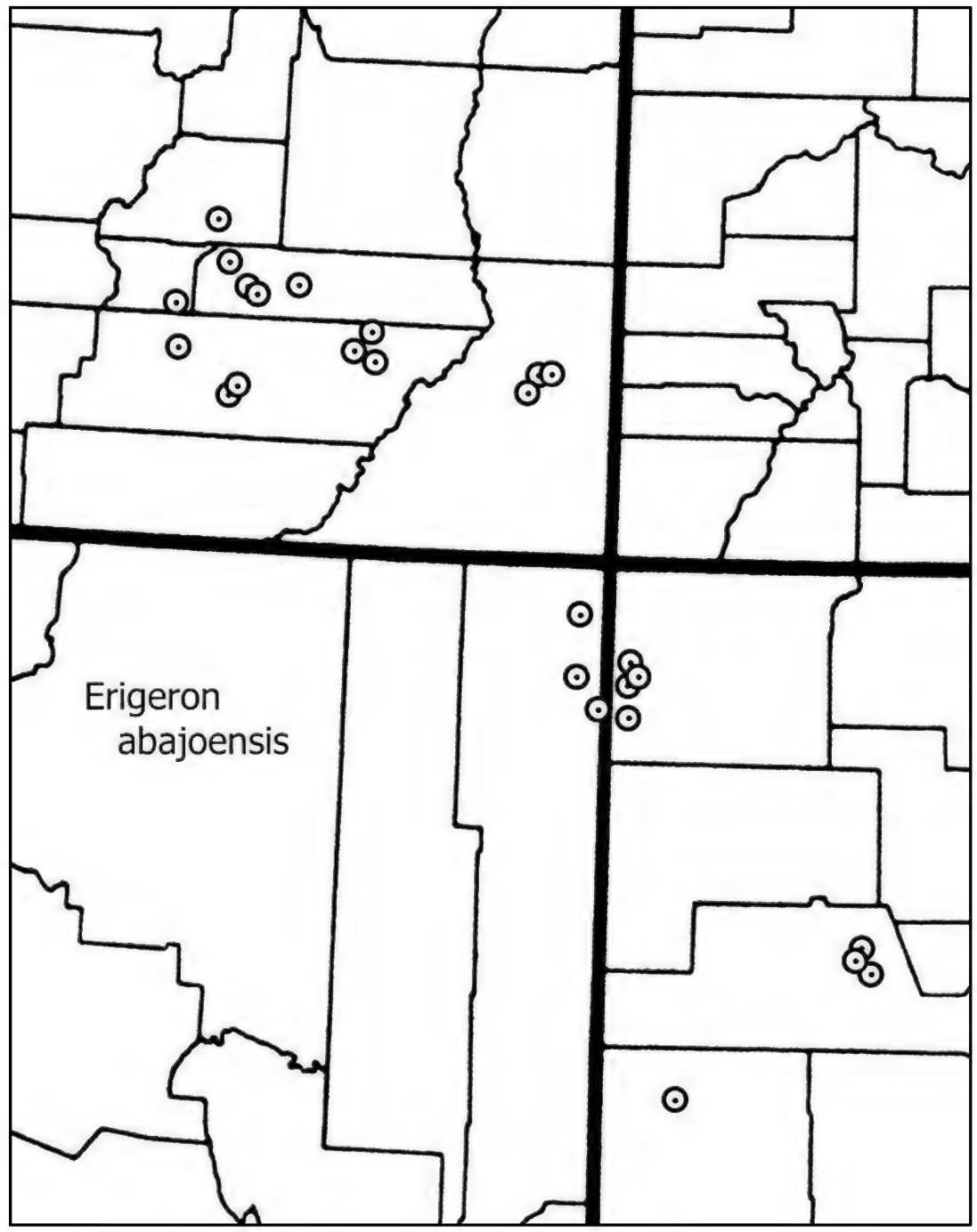

Figure 1. Distribution of *Erigeron abajoensis*.

Erigeron abajoensis Cronq., Brittonia 6: 168. 1947. **TYPE**: **Utah**. San Juan Co.: Abajo Mts (eastern range), 3000–3300 m, 17 Aug 1911, *P.A. Rydberg & A.O. Garrett 9755* (holotype: NY!, image). Figure 2.

Erigeron caespitosus var. *laccoliticus* M.E. Jones, Proc. Calif. Acad. Sci. 2, 5: 696. 1895. **TYPE**: **Utah**. San Juan Co.: Henry Mts., Marvine Laccolite, gravel, 6000 ft, 23 Jul 1894, *M.E. Jones 5661* (holotype: RSA image; isotypes: MSC image, NY image, US-2 sheets images, Fig. 3).

Erigeron awapensis S.L. Welsh, Great Basin Naturalist 43: 365. 1983. **TYPE**: **Utah**. Garfield Co.: Milepost 26.5 S of Antimony, igneous, bouldery slope in canyon, *Artemisia* community, 7000 ft, 4 Sep 1969, *S.L. & S.L. Welsh 9388* (holotype: BRY!, image). Figure 4.

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Figure 2. *Erigeron abajoensis*. San Juan Co., Utah. *Rydberg & Garrett 9755* (NY, holotype).

Figure 3. *Erigeron abajoensis*. San Juan Co., Utah. *Jones 5661* (US, isotype of *E. caespitosus* var. *laccoliticus*).

Figure 4. *Erigeron abajoensis*. Garfield Co., Utah. *Welsh 9388* (BRY, holotype of *E. awapensis*).

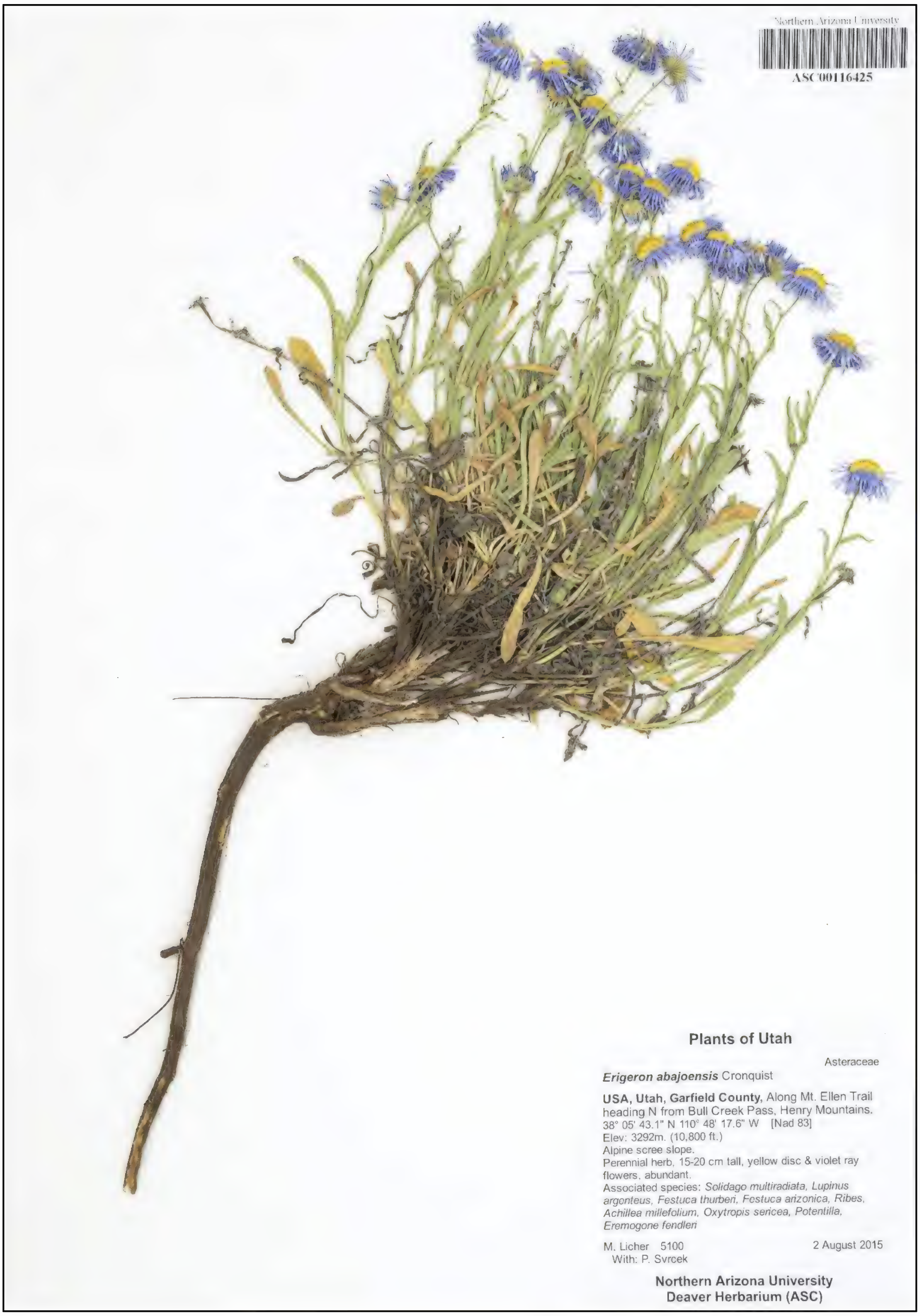

Figure 5. *Erigeron abajoensis*. Garfield Co., Utah. *Licher 5100* (ASC).

Figure 6. *Erigeron abajoensis*. San Juan Co., Utah. *Atwood 7055* (BRY).

Figure 7. *Erigeron abajoensis*. Wayne Co., Utah. *Welsh & Atwood 26274* (BRY).

Figure 8. *Erigeron abajoensis*. San Juan Co., New Mexico. *Rink 9840* (ASC).

Figure 9. *Erigeron abajoensis*. San Juan Co., New Mexico. *Heil et al. 24133* (NAVA).

Figure 10. *Erigeron abajoensis*. Catron Co., New Mexico. *McIntosh 1400* (NY).

Figure 11. *Erigeron abajoensis*. Apache Co., Arizona. *Goodman & Payson 2915* (NY).

Figure 12. *Erigeron abajoensis*. Cibola Co., New Mexico. *Castetter 7887* (UNM).

Figure 13. *Erigeron abajoensis*. Cibola Co., New Mexico. *Ivey s.n.* (UNM).

Figure 14. *Erigeron abajoensis*. Cibola Co., New Mexico. *Martin 3383* (UNM).

Figure 15. *Erigeron abajoensis*. Knoll above Robertson Pasture Trail, Abajo Mountains, 10,600 ft, 20 July 2016. Photo by Al Schneider, Southwest Colorado Wildflowers. Nodding buds are prominent.

Figure 16. *Erigeron abajoensis*. Knoll above Robertson Pasture Trail, Abajo Mountains, 10,600 ft, 8 July 2020. Photo by Al Schneider. Nodding buds, reflexing ray ligules.

Figure 17. *Erigeron abajoensis*. Prairie Dog Knoll, Abajo Mountains, 9800 ft, 17 August 2009. Photo by Al Schneider, Southwest Colorado Wildflowers. Ligules of ray corollas sharply reflexing at fruit maturity — this behavior shows on herbarium specimens as well.

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REVISED SUBTRIBAL CLASSIFICATION OF ASTEREAE (ASTERACEAE)

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ABSTRACT

In the classification proposed here, tribe Astereae includes 252 genera, arranged in 36 subtribes. Twenty (20) new subtribes are described: **Afroasterinae**, **Celmisiinae**, **Chamaegerinae**, **Chiliotrichinae**, **Denekiinae**, **Doellingeriinae**, **Egletinae**, **Eschenbachiinae**, **Formaniinae**, **Geissolepinae**, **Gutierreziinae**, **Ionactinae**, **Iranoasterinae**, **Oclemeninae**, **Oritrophiinae**, **Madagasterinae**, **Mairiinae**, **Nannoglottidinae**, **Printziinae**, and **Pteroniinae**. Six new combinations at specific rank are made: **Eschenbachia gouanii** (L.) Nesom, **comb. nov.**, **Eschenbachia subscaposa** (O. Hoffm.) Nesom, **comb. nov.**, **Eschenbachia tigrensis** (Oliv. & Hiern.) Nesom, **comb. nov.**, and **Eschenbachia ulmifolia** (Burm. f.) Nesom, **comb. nov.**; **Psiadia ageratoides** (DC.) Nesom, **comb. nov.** and **Psiadia humilis** (Humbert) Nesom, **comb. nov.**

Earlier subtribal arrangements for Astereae (Zhang & Bremer 1993; Bremer 1994; Nesom 1994a; Nesom & Robinson 2007) were based mostly on morphology, predating a surge of molecular-taxonomic studies that show that the earlier classifications were often far from the mark. Many groups were polyphyletic and relatively smaller natural groups often were misplaced or proved to be more phyletically isolated than thought. Geographic proximity, in particular, has proved to be a more effective indicator of evolutionary relationship than recognized previously.

As part of the development of an updated account of Astereae genera (CWG 2020; Nesom 2020a), a subtribal arrangement is useful in conceptualizing patterns of evolutionary relationships and facilitating reference to groups of genera and species. The taxonomy presented here draws from molecular studies and hopefully aids in summarizing those studies as well as providing as a hypothetical taxonomic framework. Generic boundaries in many species groups remain to be clearly delimited and new genera remain to be described. Polyphyletic or otherwise non-monophyletic subgroups are indicated in the classification.

The concept of subtribe used here is subjective. Distinctive and evolutionarily isolated genera, especially those in primitive positions, are treated as monotypic subtribes. Some groups of genera are morphologically coherent and are given subtribal rank. On the other hand, some subtribes recognized here comprise morphologically diverse groups that would not have been seen as monophyletic except for the molecular data — subtribes segregated from these might justifiably be recognized.

Major lineages or groups of Astereae are indicated on Figure 1:

Basal grade, including isolated genera, the South American-Oceania group of Chiliotrichinae/ Celmisiinae/Oritrophiinae, the mainly African Homochrominae/Pteroniinae and Eschenbachiinae, and the group of woody genera from Madagascar (Madagasterinae).

Bellis lineage, including the Eurasian Bellidinae and Chamaegerinae and the primarily African Grangeinae.

Aster lineage, including the Asian Asterinae and major Australian-Oceania groups (Lagenophorinae, and Brachyscominae — the relative positions of these four groups are unresolved, even though they are specified (speculatively) in Fig. 1). Figure 2 summarizes hypothetical relationships among the genera and groups of Asterinae.

Baccharis lineage, including the mostly South American Baccharidinae, Podocominae, and Hinterhuberinae, merged here into a single subtribe, Baccharidinae. Sister to the North American lineage. Figure 3 summarizes hypothetical relationships among genera and groups of Baccharidinae.

North American lineage, including the diverse array of subtribes that radiated mostly in Mexico and the USA, with some groups spreading into South America.

Table 1 gives an alphabetical list of the Astereae subtribes with the linear sequence number for each. Table 2 lists all genera of Astereae accepted here, with the subtribal assignment for each.

Construction of the phylogenetic diagrams

The phylogenetic diagrams (Figs. 1–3) might be thought of as intuitively constructed consensus trees, summarizing published phylogenetic analyses based on DNA sequence data. They are working hypotheses. The diagram position of some taxa is speculative, reflecting a subjective choice from among ambiguous placements in molecular phylogenies. Species included in molecular analyses are indicated in the classification within square brackets. Species and genera not included in molecular analyses are placed on the basis of morphology and geography.

Published molecular analyses of Astereae vary widely in the genera and species included, and phylogenetic patterns indicated among various cladograms are often obscure. The series of cladograms published by Brouillet et al. (2009) is the most complete in providing an overview of the whole tribe, but many additional studies have been published subsequently and these additional insights have been considered.

Subtribes in the linear classification are numbered consecutively and mostly arranged alphabetically within major geographic regions — North America/Central America, South America, Oceania, Eurasia, and Africa/Madagascar/SE Asia. The linear arrangement is not intended to show relationships among subtribes. In Figures 1 and 2, the number for each subtribe matches that in the consecutive numbering of the linear arrangement.

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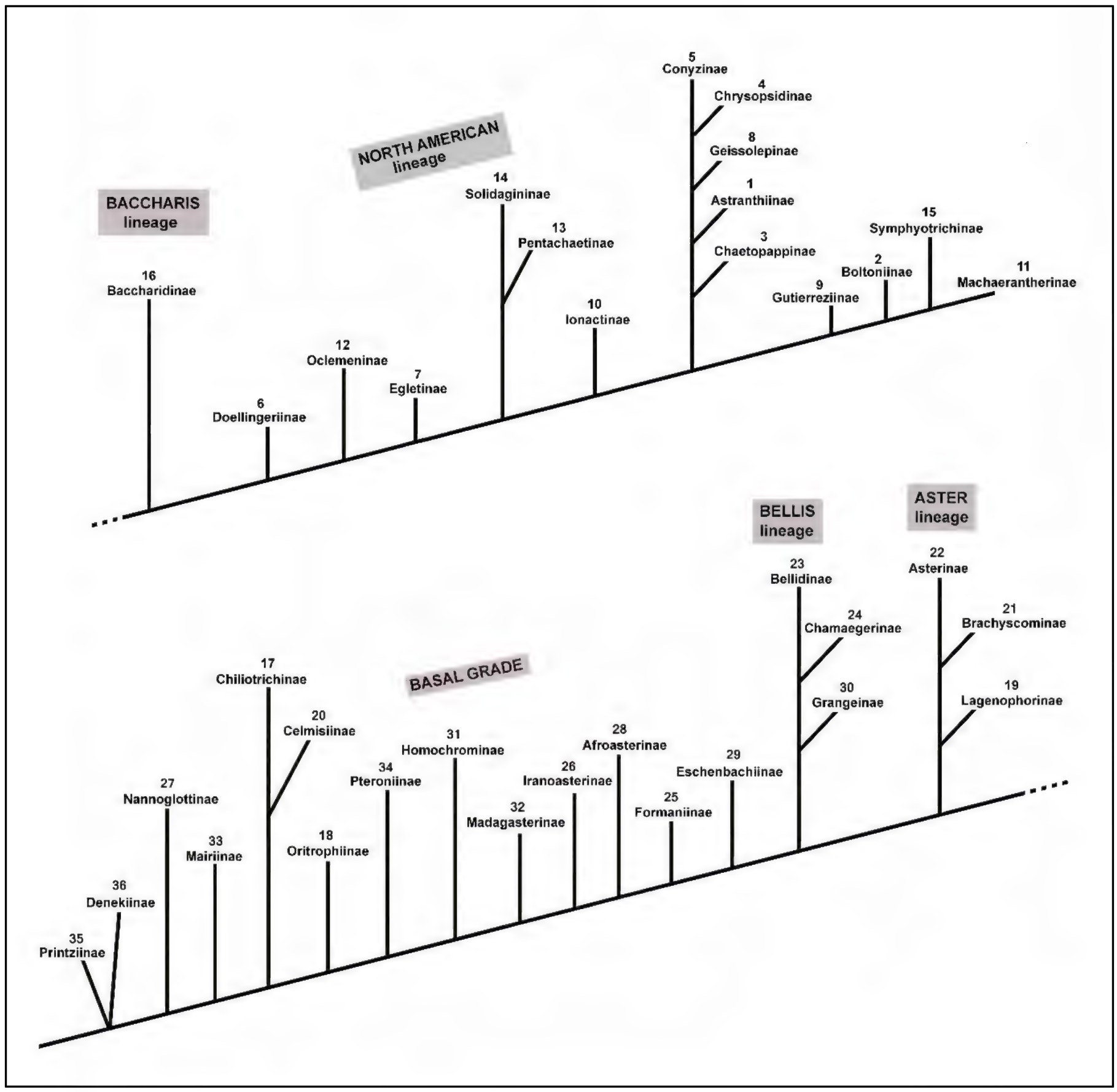

Figure 1. Hypothetical subtribal phylogeny of Astereae. See "Construction of the phylogenetic diagrams" in the introduction. Most, if not all, published trees have been studied as the basis for this intuitively constructed diagram. It is an approximation and hopefully will serve at least as a guide for further analyses.

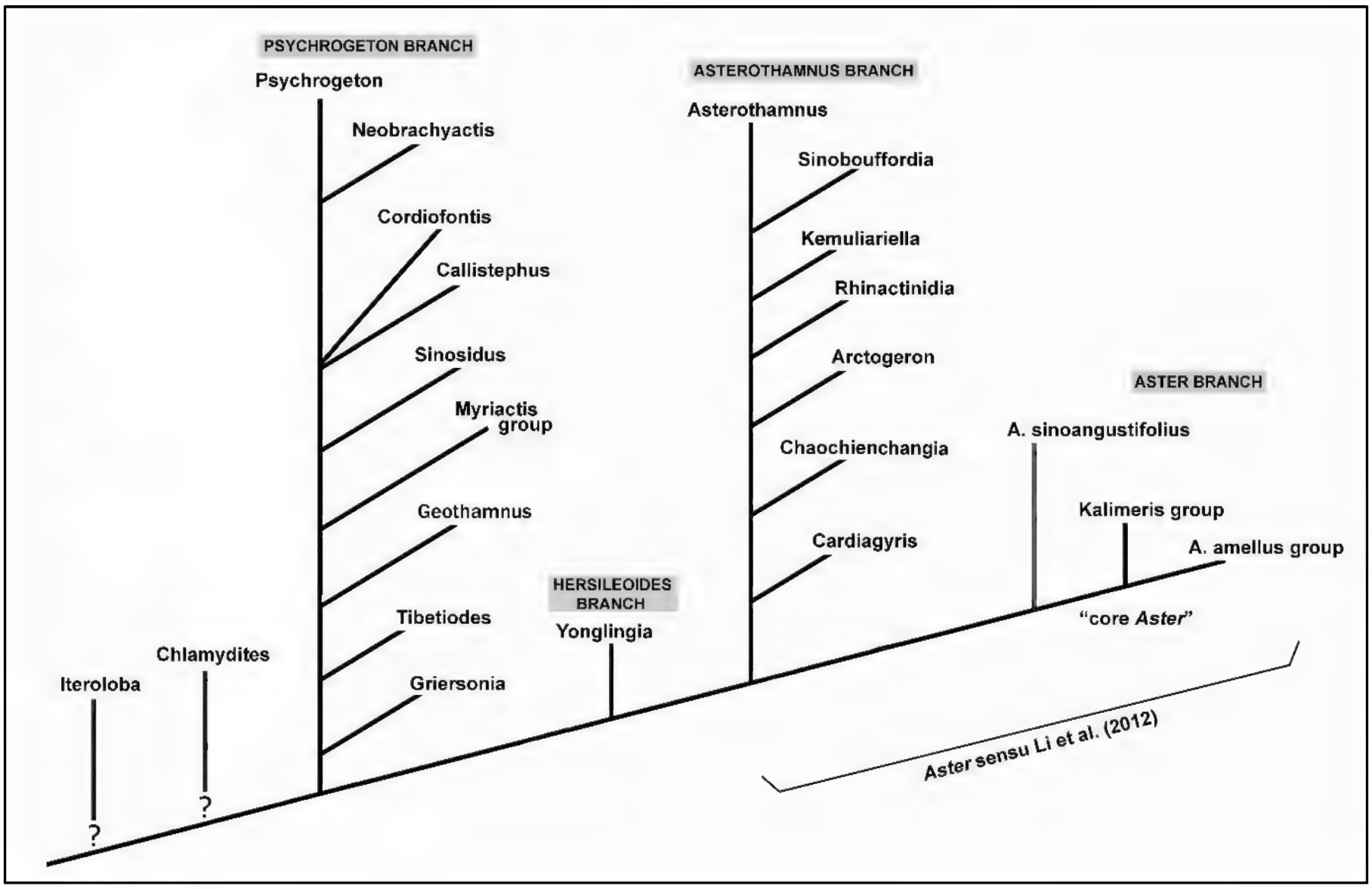

Figure 2. Hypothetical phylogeny of genera and groups of genera of subtribe Asterinae. The Kalimeris group includes *Sheareria*, *Kalimeris*, *Heteropappus*, *Aster* sect. *Ageratoides*, and a clade sister to sect. *Ageratoides*. The Aster amellus group includes *Aster* sensu stricto, *Miyamayomena*, *Rhynchospermum*, *Turczaninovia*, and a diverse group of unplaced species. *Aster sinoangustifolius* is sister to the rest of "core *Aster*." Li et al. (2012) considered the *Asterothamnus* branch as part of *Aster* sensu stricto.

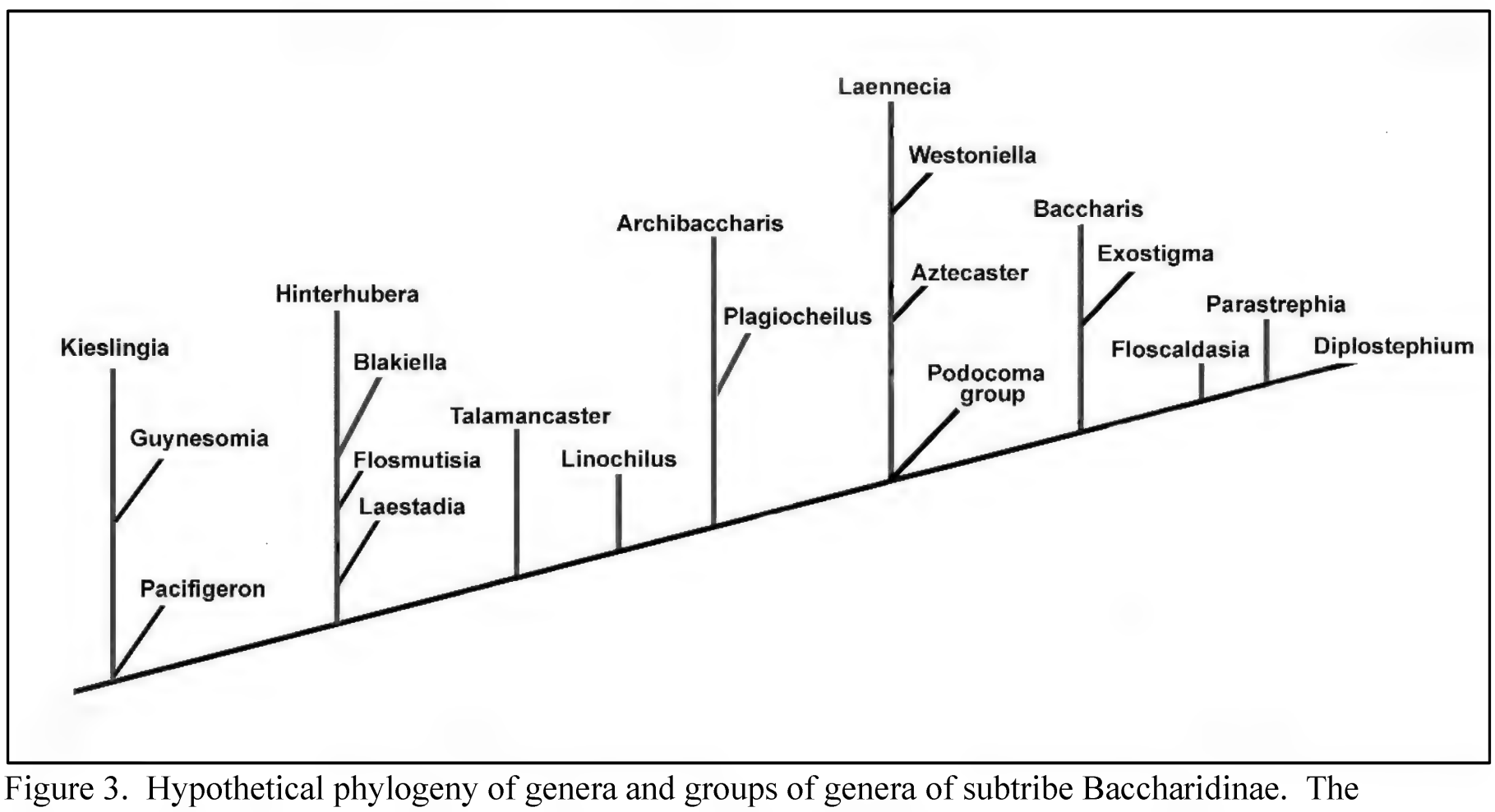

Figure 3. Hypothetical phylogeny of genera and groups of genera of subtribe Baccharidinae. The Podocoma group includes *Podocoma, Asteropsis*, *Inulopsis*, *Microgyne*, and *Sommerfeltia*. Genera previously treated within Hinterhuberinae and Podocominae are included within the Baccharidinae.

Table 1. Subtribes of Astereae. Numbers refer to sequence in the linear classification.

Afroasterinae 28
Astranthiinae 1
Asterinae 22
Baccharidinae 16
Bellidinae 23
Boltoniinae 2
Brachyscominae 21
Celmisiinae 20
Chamaegerinae 24
Chiliotrichinae 17
Chaetopappinae 3
Chrysopsidinae 4
Conyzinae 5
Denekiinae 36
Doellingeriinae 6
Egletinae 7
Eschenbachiinae 29
Formaniinae 25
Geissolepinae 8
Grangeinae 30
Gutierreziinae 9
Homochrominae 31
Ionactinae 10
Iranoasterinae 26
Lagenophorinae 19
Machaerantherinae 11
Madagasterinae 32
Mairiinae 33
Nannoglottidinae 27
Oclemeninae 12
Oritrophiinae 18
Pentachaetinae 13
Printziinae 35
Pteroniinae 34
Solidagininae 14
Symphyotrichinae 15

Table 2. Genera of Astereae.

Acamptopappus (A. Gray) A. Gray Solidagininae
Achnophora F. Muell. Brachyscominae
Afroaster Manning & Goldblatt Afroasterinae
Akeassia Lebrun & Stork Grangeinae
Almutaster Löve & Löve Symphyotrichinae
Amellus L. Homochrominae
Ampelaster Nesom Symphyotrichinae
Amphiachyris (DC.) Nutt. Guttieriziinae
Amphipappus Torr. & Gray ex Gray Solidagininae
Aphanostephus DC. Conyzinae
Apodocephala J. Baker Madagasterinae
Apopyros Nesom Conyzinae
Aquilula Nesom Gutierriziinae
Archibaccharis Heering Baccharidinae
Arctogeron DC. Asterinae
Aster L. Asterinae
Asteropsis Less. Baccharidinae
Asterothamnus Novopokr. Asterinae
Astranthium Nutt. Astranthiinae
Aylacophora Cabrera Chiliotrichinae
Aztecaster Nesom Baccharidinae
Baccharis L. Baccharidinae
Bathysanthus Nesom Solidagininae
Batopilasia Nesom & Noyes Boltoniinae
Bellidiastrum Scop. Bellidinae
Bellis L. Bellidinae
Bellium L. Bellidinae
Benitoa Keck Machaerantherinae
Bigelowia DC. Gutierreziinae
Blakiella Cuatrec. Baccharidinae
Boltonia L'Hér. Boltoniinae
Brachyscome Cass. Brachyscominae
Bradburia Torr. & Gray Chrysopsidinae
Brintonia Greene Solidagininae
Cabreraea Bonif. Chiliotrichinae
Callistephus Cass. Asterinae
Calotis R. Br. Brachyscominae
Camptacra Burb. Brachyscominae
Canadanthus Nesom Symphyotrichinae
Cardiagyris Nesom Asterinae
Celmisia Cass. Celmisiinae
Ceratogyne Turcz. Brachyscominae
Ceruana Forssk. Grangeinae
Chaetopappa DC. Chaetopappinae
Chamaegeron Schrenk Chamaegerinae
Chaochienchangia Nesom Asterinae
Chiliophyllum Phil. Chiliotrichinae
Chiliotrichiopsis Cabrera Chiliotrichinae
Chiliotrichum Cass. Chiliotrichinae
Chlamydites J.R. Drummond Asterinae
Chloracantha Nesom et al. Boltoniinae
Chondropyxis D.A. Cooke Brachyscominae
Chrysocoma L. Homochrominae
Chrysoma Nutt. Solidagininae
Chrysopsis (Nutt.) Ell. Chrysopsidinae
Chrysothamnus Nutt. Solidagininae
Colobanthera Humbert Grangeinae
Columbiadoria Nesom Solidagininae
Commidendrum Burch. ex DC. Homochrominae
Cordiofontis Nesom Asterinae

Corethrogyne DC. Machaerantherinae
Crinitina Soják Bellidinae
Croptilon Raf. Chrysopsidinae
Cuniculotinus Urbatsch et al. Solidagininae
Dacryotrichia Wild Grangeinae
Damnamenia Given Celmisiinae
Denekia Thunb. Denekiinae
Dichaetophora A. Gray Astranthiinae
Dichrocephala L'Hér. ex DC. Grangeinae
Dichromochlamys Dunlop Brachyscominae
Dieteria Nutt. Machaerantherinae
Dimorphocoma Muell. & Tate Brachyscominae
Diplostephium Kunth Baccharidinae
Doellingeria Nees Doellingeriinae
Eastwoodia Brandeg. Solidagininae
Egletes Cass. Egletinae
Elachanthus F. Muell. Brachyscominae
Engleria O. Hoffm. Homochrominae
Eoglandula Nesom Brachyscominae
Ephedrides Nesom Brachyscominae
Ericameria Nutt. Pentachaetinae
Erigeron L. Conyzinae
Erodiophyllum F. Muell. Brachyscominae
Eschenbachia Moench. Eschenbachiinae
Eucephalus Nutt. Doellingeriinae
Eurybia (Cass.) Gray Machaerantherinae
Euthamia (Nutt.) Cass. Gutierreziinae
Exostigma Sancho Baccharidinae
Felicia Cass. Homochrominae
Floscaldasia Cuatrec. Baccharidinae
Flosmutisia Cuatrec. Baccharidinae
Formania W. Smith & J. Small Formaniinae
Galatella (Cass.) Cass. Bellidinae
Geissolepis B.L. Rob. Geissolepidinae
Geothamnus Nesom Asterinae
Grangea Adans. Grangeinae
Grangeopsis Humbert Grangeinae
Grauanthus Fayed Grangeinae
Griersonia Nesom Asterinae
Grindelia Willd. Machaerantherinae
Gundlachia A. Gray Gutierreziinae
Gutierrezia Lag. Gutierreziinae
Guynesomia Bonif. & Sancho Baccharidinae
Gymnosperma Less. Gutierreziinae
Gymnostephium Less. Homochrominae
Gyrodoma Wild Grangeinae
Haplopappus Cass. Machaerantherinae
Haroldia Bonif. Chiliotrichinae
Hazardia Greene Machaerantherinae
Heleodeaster Nesom Asterinae
Herrickia Woot. & Standl. Machaerantherinae
Heteromma Benth. Homochrominae
Heteropappus Less. Asterinae
Heteroplexis C.C. Chang Grangeinae
Heterotheca Cass. Chrysopsidinae
Hinterhubera Sch.Bip. ex Wedd. Baccharidinae
Hullsia P.S. Short Brachyscominae
Hysterionica Willd. Conyzinae
Inulopsis (DC.) O. Hoffm. Baccharidinae
Ionactis Greene Chaetopappinae
Iotasperma Nesom Brachyscominae
Iranoaster Kaz.-Osaloo et al. Iranoasterinae
Isocoma Nutt. Machaerantherinae
Isoetopsis Turcz. Brachyscominae
Iteroloba Nesom Asterinae
Ixiochlamys Muell. & Sond. Brachyscominae
Jeffreya Wild Homochrominae
Kalimeris (Cass.) Cass. Asterinae
Katinasia Bonif. Chiliotrichinae
Kemulariella Tamamsch. Asterinae
Keysseria Lauterb. Lagenophorinae
Kieslingia Faundez et al. Chiliotrichinae
Kippistia F. Muell. Brachyscominae
Kitamuria Nesom Bellidinae
Lachnophyllum Bunge Chamaegerinae
Laennecia Cass. Baccharidinae
Laestadia Kunth ex Less. Baccharidinae
Lagenocypsela Swenson & Bremer Lagenophorinae
Lagenophora Cass. Lagenophorinae
Landerolaria Nesom Brachyscominae
Lepidophyllum Cass. Chiliotrichinae
Leptostelma D. Don Conyzinae
Lessingia Cham. Machaerantherinae
Leucosyris Greene Machaerantherinae
Linealia Nesom Brachyscominae
Linochilus Benth. Baccharidinae
Llerasia Triana Chiliotrichinae
Lorandersonia Urbatsch et al. Solidagininae
Machaeranthera Nees Machaerantherinae
Madagaster Nesom Madagasterinae
Mairia Nees Mairiinae
Medranoa Urbatsch & Roberts Gutierreziinae
Melanodendron DC. Homochrominae
Metamyriactis Nesom Asterinae
Microglossa DC. Grangeinae
Microgyne Less. Baccharidinae
Minuria DC. Brachyscominae
Miyamayomena Kitam. Asterinae
Monoptilon Torr. & Gray Chaetopappinae
Mtonia Beentje Grangeinae
Muellerolaria Nesom Brachyscominae
Myriactis Less. Asterinae
Nannoglottis Maxim. Nannoglottidinae

Nardophyllum (Hook. & Arn.) Hook. & Arn. Chiliotrichinae
Neja D. Don Conyzinae Conyzinae
Neobrachyactis Brouillet Asterinae
Neolaria Nesom Brachyscominae
Nestotus Roberts et al. Solidagininae
Nidorella Cass. Grangeinae
Nolletia Cass. Homochrominae
Noticastrum DC. Chrysopsidinae
Notopappus Klingenb. Machaerantherinae
Novaguinea D.J.N. Hind Lagenophorinae
Novenia S.E. Freire Oritrophiinae
Oclemena Greene Oclemeninae
Ocyroe Phil. Chiliotrichinae
Olearia Moench Brachyscominae
Oligoneuron Small Solidagininae
Oonopsis (Nutt.) Greene Machaerantherinae
Oreochrysum Rydb. Solidagininae
Oreostemma Greene Machaerantherinae
Oritrophium (Kunth) Cuatrec. Oritrophiinae
Osbertia Greene Chrysopsidinae
Pachystegia Cheeseman Celmisiinae
Pacifigeron Nesom Baccharidinae
Pappochroma Raf. Brachyscominae
Parastrephia Nutt. Baccharidinae
Pentachaeta Nutt. Pentachaetinae
Peripleura (Burb.) Nesom Brachyscominae
Petradoria Greene Solidagininae
Phaseolaria Nesom Brachyscominae
Pilbara Lander Brachyscominae
Piora J. Kost. Lagenophorinae
Pityopsis Nutt. Chrysopsidinae
Plagiocheilus Arn. ex DC. Baccharidinae
Pleurophyllum Hook. f. Celmisiinae
Podocoma Cass. Baccharidinae
Poecilolepis Grau Homochrominae
Polyarrhena Cass. Homochrominae
Printzia Cass. Printziinae
Psiadia Jacq. ex Willd. Grangeinae
Psilactis A. Gray Symphyotrichinae
Psychrogeton Boiss. Asterinae
Pteronia L. Pteroniinae
Pyrrocoma Hook. Machaerantherinae
Pytinicarpa Nesom Lagenophorinae
Rayjacksonia Hartm. & Lane Machaerantherinae
Remya Hillebr. ex Benth. & Hook. f. Brachyscominae
Rhamphogyne S. Moore Grangeinae
Rhinactinidia Novopokr. Asterinae
Rhynchospermum Reinw. ex Reinw. Asterinae
Rigiopappus A. Gray Pentachaetinae
Rochonia DC. Madagasterinae
Roodebergia B. Nord. Homochrominae
Sanrobertia Nesom Symphyotrichinae
Sericocarpus Nees Solidagininae
Sheareria S. Moore Asterinae
Sinobouffordia Nesom Asterinae
Sinosidus Nesom Asterinae
Solenogyne Cass. Lagenophorinae
Solidago L. Solidagininae
Sommerfeltia Less. Baccharidinae
Stenotus Nutt. Solidagininae
Stephanodoria Greene Machaerantherinae
Symphyotrichum Nees Symphyotrichinae
Talamancaster Pruski Baccharidinae
Tetramolopium Nees Brachyscominae
Thespis DC. Eschenbachiinae
Thurovia Rose Gutierreziinae
Tibetiodes Nesom Asterinae
Toiyabea Roberts et al. Solidagininae
Tomentaurum Nesom Chrysopsidinae
Tonestus A. Nels. Solidagininae
Townsendia Hook. Astranthiinae
Tracyina S.F. Blake Pentachaetinae
Triniteurybia Brouillet et al. Machaerantherinae
Tripolium Nees Bellidinae
Turczaninovia DC. Asterinae
Vernoniopsis Humbert Madagasterinae
Vittadinia A. Rich. Brachyscominae
Walsholaria Nesom Brachyscominae
Welwitschiella Engler Grangeinae
Westoniella Cuatrec. Baccharidinae
Wollemiaster Nesom Brachyscominae
Xanthisma DC. Machaerantherinae
Xanthocephalum Willd. Machaerantherinae
Xylorhiza Nutt. Machaerantherinae
Xylothamia Nesom et al. Gutierreziinae
Yonglingia Nesom Asterinae
Zyrphelis Cass. Homochrominae

SUBTRIBAL CLASSIFICATION OF ASTEREAE

The Astereae includes ca. 3100 species, distributed primarily in temperate regions. The group is characterized by ecaudate, non-calcarate anther bases (a few primitive genera have caudate bases) and disc floret styles with separated, marginal stigmatic lines and deltate to triangular or lanceolate style appendages glabrous adaxially, with sweeping hairs abaxially.

NORTH AMERICA /CENTRAL AMERICA

1. ASTRANTHIINAE Nesom, Sida 19: 265. 2000.
Astranthium Nutt. [*Astranthium integrifolium*]
Dichaetophora A. Gray [*Dichaetophora campestris*] Monotypic.
Townsendia Hook. [*Townsendia florifer*]

2. BOLTONIINAE Nesom, Sida 19: 266. 2000.
Batopilasia Nesom & Noyes [*Batopilasia byei*] Monotypic.
Boltonia L'Hér. [*Boltonia asteroides*, *B. diffusa*]
Chloracantha Nesom [*Chloracantha spinosa*]

3. CHAETOPAPPINAE Nesom, Sida 19: 264. 2000.
Chaetopappa DC. [*Chaetopappa bellioides*, *C. effusa*, *C. ericoides*]
Monoptilon Torr. & Gray [*Monoptilon bellioides*]

4. CHRYSOPSIDINAE Nesom, Phytologia 76: 203. 1994.
Bradburia Torr. & Gray [*Bradburia hirtella*, *B. pilosa*]
Chrysopsis (Nutt.) Elliott [*Chrysopsis delaneyi*, *C. dressei*, *C. godfreyi*, *C. gossypina*, *C. highlandsensis*, *C. lanuginosa*, *C. linearifolia*, *C. mariana*, *C. scabrella*, *C. subulata*]
Croptilon Raf. [*Croptilon divaricatam*, *C. rigidifolium*]
Heterotheca Cass. [*Heterotheca camporum*, *H. horrida*, *H. jonesii*, *H. oregona*, *H. shevockii*, *H. subaxillaris*, *H. rutteri*, *H. villosa*, *H. viscida*, *H. zionensis*]
Noticastrum DC. [*Noticastrum marginatum*]
Osbertia Greene [*Osbertia stolonifera*] See Morgan and Simpson (1992).
Pityopsis Nutt. [*Pityopsis aspera*, *P. falcata*, *P. flexuosa*, *P. graminifolia*, *P. pinifolia*]
Tomentaurum Nesom Monotypic, not included in molecular sampling.

See Nesom (1991a) for a cladistic analysis of Chrysopsidinae based on morphological characters.

5. CONYZINAE Horan., Char. Ess. Fam., 93. 1847.
Aphanostephus DC. [*Aphanostephus ramosissimus*, *A. skirrhobasis*]
Apopyros Nesom [*Apopyros warmingii*]
Erigeron L. (including *Conyza* L. *sensu* stricto) [many species; see Noyes 2000]
Hysterionica Willd. [*Hysterionica jasionoides*]
Leptostelma D. Don [*Leptostelma maxima*]
Neja D. Don [*Neja filiformis*]

In a strict application of monophyly, all species of Conyzinae would be identified as *Erigeron* (Noyes 2000). Species identified as *Conyza* have arisen evolutionarily from within *Erigeron* at least twice. *Apopyros*, *Hysterionica*, *Leptostelma*, and *Neja* are distinctive monophyletic groups of "austro-brasilien" South America most closely related to *Conyza* (*Erigeron*) *bonariensis*, *Conyza* (*Erigeron*) *primulifolia*, and probably most of the South American conyzas, to South American *Erigeron* species, and to several groups of Mexican *Erigeron*. *Aphanostephus*, a genus of the southwestern USA and Mexico, was not suspected of close relationship to *Erigeron* until molecular analysis showed it so. See further commentary in Nesom (2020b).

6. DOELLINGERIINAE Nesom, **subtr. nov. TYPE**: *Doellingeria* Nees

Perennial herbs (fibrous-rooted in *Doellingeria*, rhizomatous in *Eucephalus*) with scale-like basal and lower cauline leaves; leaves eglandular; capitulescence corymbiform to paniculiform; phyllaries strongly graduate in length, rounded (*Doellingeria*) or keeled (*Eucephalus*); rays absent or relatively few (2–20), white to violet; achenes eglandular, broadly columnar with 5–9 resinous veins (*Doelllingeria*) or strongly flattened and 2-nerved (*Eucephalus*); pappus bristles in 2–4 subequal series, apices clavate.

Doellingeria Nees [genus of 3 species, eastern USA; all included by Allen et al.]
Eucephalus Nutt. [genus of 10 species, western USA; all included by Allen et al.]

All 13 species of this group have been united as *Doellingeria* (Allen et al. 2019), based on molecular analyses showing *Doellingeria* and *Eucephalus elegans* as a sister group to the rest of *Eucephalus* (ITS/ETS sequences) or as considerably more distantly related to the rest of *Eucephalus* (chloroplast sequences). The nuclear sequences suggest that the *Doellingeria* species arose as a derived lineage from within *Eucephalus*, while (as noted by Allen et al.) the plastid sequences suggest a more complex evolutionary history in the origin of *Doellingeria* and *Eucephalus*, involving species of the group identified here as Baccharidinae. Their taxonomic option was based on the nuclear sequences.

Doellingeria and *Eucephalus*, in any case, are widely separated in geography and discontinuously distinct in morphology and there is nothing in *E. elegans* to suggest that it is closest to *Doellingeria*. The gain in considering the two groups congeneric seems outweighed by evolutionary information conveyed by maintaining them as separate.

7. EGLETINAE Nesom, subtr. nov. TYPE: *Egletes* Cass.

Taprooted, annual herbs, glandular-resinous; leaves pinnatifid to bipinnatifid to lobed or toothed; receptacles conical; disc flowers bisexual, corollas 3–5-lobed; ray flowers multiseriate (usually 2–4 series) with white, filiform ligules; achenes compressed, 2-nerved, faces usually glandular; pappus absent, the achene apex extended into a whitish, cartilaginous crown or cup, this sometimes broad and flaring.

Egletes Cass. [*Egletes liebmannii*]

Egletes comprises about 6 species from South America though Central America and Mexico into the southern USA. It was earlier placed (Nesom 1994a) in the mostly African Grangeinae, with which its features seem closely aligned, but molecular data indicate that *Egletes* arose from within the North American clade and similarities to Grangeinae apparently are convergent. Fayed (1979) included *Egletes* in his revision of Grangeinae but concluded that it did not belong there.

8. GEISSOLEPINAE Nesom, **subtr. nov. TYPE**: *Geissolepis* B.L. Rob.

Perennial, stoloniferous herbs with prostrate stems; leaves succulent, linear-oblanceolate; receptacles steeply conic, paleate; ray flowers 8–12, ligules white; disc flowers bisexual, fertile; achenes 3–4-angled, with ca. 8 orange-resinous ribs, faces with glochidiate (anchor-shaped) duplex hairs; pappus of 6–8 narrow pales with uncinate-ciliate margins.

Geissolepis B.L. Rob. [*Geissolepis suaedifolia*]

Geissolepis, a monotypic Mexican endemic, was earlier regarded (Nesom 1994a) as closely related to *Astranthium* and *Townsendia*, with which it shares a conical receptacle, reduced pappus, and glochidiate achenial hairs, but molecular data indicate that it is a basal element in the North American clade, its evolutionary affinity ambiguous.

9. GUTIERREZIINAE Nesom, **subtr. nov. TYPE**: *Gutierrezia* Lag.

Shrubs, subshrubs, or annual or perennial herbs; leaves punctate-glandular, mostly sessile, 1-nerved or with 3–5 parallel veins; disc flowers 2–30(–50) in *Gundlachia*), anther filaments inserted at the junction of the corolla tube and limb (vs. well below the tube apex); ray flowers yellow, rarely white; achenes subterete, (2–)4–10 nerved, sparsely to densely strigose, eglandular; pappus or bristles or scales or absent.

Amphiachyris (DC.) Nutt. [*Amphiachyris dracunculoides*]
Aquilula Nesom [*Aquilula riskindii*] Monotypic.
Bigelowia DC. [*Bigelowia nudata*, *B. nuttallii*]
Euthamia (Nutt.) Cass. [*Euthamia graminifolia*, *E. leptocephala*, *E. occidentalis*, *E. tenuifolia*]
Gundlachia A. Gray [*Gundlachia corymbosa*]
Gutierrezia Lag. [*Gutierrezia sarothrae*, *G. texana*]
Gymnosperma Less. [*Gymnosperma glutinosa*] Monotypic.
Medranoa Urbatsch & Roberts (incl. *Chihuahuana*, *Neonesomia*, and *Xylovirgata*) [*Medranoa johnstonii*, *M. palmeri*, *M. parrasana*, *M. pseudobaccharis*]
Thurovia Rose [*Thurovia triflora*] Monotypic.
Xylothamia Nesom, Suh, Morgan, & Simpson [*Xylothamia diffusa*, *X. triantha*, *X. truncata*]

These genera were previously placed (Nesom 1994a) in the Solidagininae although their unity as a natural group was earlier recognized (Suh 1989; Suh & Simpson 1990; Nesom et al. 1990; Nesom 1991b). See Nesom (2018c) for a taxonomic summary of *Aquilula*, *Gundlachia*, *Medranoa*, and *Xylothamia*.

10. IONACTINAE Nesom, **subtr. nov. TYPE**: *Ionactis linariifolia* Greene

Perennial herbs from thick taproots and woody caudex, rarely rhizomatous; leaves cauline, stiff, narrow, 1-nerved; heads 1 or few in loose corymbs; phyllaries strongly keeled, without herbaceous tips; ray flowers 8–21, ligules violet to bluish or white, coiling; disc flowers bisexual, fertile (one species functionally staminate); achenes narrowly obovate, compressed, in rays (2–)3-nerved, in disc florets 2(–4)-nerved, strigose to sericeous (1 species glandular); pappus bristles 1–2-seriate, apically acute, outer series of short bristles or scales.

Ionactis Greene [*Ionactis caelestis*, *I. elegans*, *I. linariifolia*, *I. stenomeres*]

The position of *Ionactis* is largely unresolved in molecular phylogenies. One species is widespread in the eastern USA (*I. linariifolia*, the type); the other 4 are from the western USA.

11. MACHAERANTHERINAE Nesom, Phytologia 76: 208. 1994.

*Basal grade
Eurybia (Cass.) Gray [*Eurybia avita*, *E. chlorolepis*, *E. divaricata*, *E. eryngiifolia*, *E. furcata*, *E. gracilis*, *E. integrifolia*, *E. paludosa*, *E. radulina*, *E. sibirica*]
Herrickia Woot. & Standl. [*Herrickia glaucescens*, *H. horrida*, *H. kingii*, *H. wasatchensis*]
Oreostemma Greene [*Oreostemma alpigenum*, *O. elatum*]
Triniteurybia Brouillet, Urbatsch, & Roberts [*Triniteurybia aberrans*] Monotypic.

These four genera form a grade basal to the "core" *Machaerantherinae* (Brouillet et al. 2009).

*Machaeranthera group
Dieteria Nutt. [*Dieteria bigelovii*, *D. canescens*]
Leucosyris Greene (= *Arida* (Hartm.) Morgan & Hartm.) [*Leucosyris blepharophylla*, *L. parviflora*, *L. riparia*, *L. turneri*]
Machaeranthera Nees [*Machaeranthera tanacetifolia*]
Oonopsis (Nutt.) Greene [*Oonopsis engelmannii*, *O. wardii*]
Xanthisma DC. [*Xanthisma blephariphyllum*, *X. coloradoense*, *X. crutchfieldii*, *X. gracile*, *X. gymnocephalum*, *X. spinulosum*, *X. stenolobum*, *X. rhizomatum*, *X. texanum*, *X. viscidum*]
Xylorhiza Nutt. [*Xylorhiza tortifolia*, *X. wrightii*]

*Haplopappus group
Haplopappus Cass. [*Haplopappus* foliosus, *H. glutinosus*, *H. macrocephalus*, *H. marginalis*, *H. paucidentatus*]
Grindelia Willd. [*Grindelia ciliata*, *G. lanceolata*, *G. nana*]

Notopappus Klingenb.
Genus of 5 species (Andean Chile and Argentina) segregrated from *Grindelia* and *Haplopappus* (Klingenberg 2007).
Hazardia Greene [*Hazardia cana*, *H. detonsa*, *H. squarrosa*, *H. whitneyi*]

*Xanthocephalum group
Isocoma Nutt. [*Isocoma acradenia*, *I. menziesii*, *I. rusbyi*, *I. tenuisecta*, *I. veneta*, *I. wrightii*]
Rayjacksonia Hartm. & Lane [*Rayjacksonia phyllocephala*]
Xanthocephalum Willd. [*Xanthocephalum gymnospermoides*]
Stephanodoria Greene [*Stephanodoria tomentella*] Monotypic.
Pyrrocoma Hook. [*Pyrrocoma clementis*, *P. crocea*, *P. lanceolata*]

*Lessingia group
Corethrogyne DC. [*Corethrogyne filaginifolia*] Monotypic.
Benitoa Keck [*Benitoa occidentalis*] Monotypic.
Lessingia Cham. [*Lessingia arachnoidea*, *L. germanorum*, *L. glandulifera*, *L. hololeuca*, *L. leptoclada*, *L. micradenia*, *L. nana*, *L. nemaclada*, *L. pectinata*, *L. ramulosa*, *L. tenuis*, *L. virgata*]

12. OCLEMENINAE Nesom, **subtr. nov.** **TYPE**: *Oclemena* Greene
Perennial herbs with scale-like basal and lower cauline leaves; leaves gland-dotted; capitulescence loosely corymbiform, buds and young heads on arching-nodding peduncles; phyllaries graduate in length, linear-lanceolate, evenly herbaceous, slightly keeled; achenes densely glandular, fusiform to narrowly obovate or oblong, 4–8-nerved; pappus bristles in 2–3 subequal series, the outer series sometimes short, apices acute.

Oclemena Greene [*Oclemena acuminata*, *O. nemoralis*, *O. reticulata*]

Molecular data (e.g., Brouillet et al. 2009) indicate that *Oclemena* is without close relatives in the North American clade and in a relatively basal but phylogenetically unresolved position. One of the three species has been formally treated within *Doellingeria*, which also produces a corymboid capitulescence and scale-like basal and lower cauline leaves, but it did not belong there.

13. PENTACHAETINAE Nesom, Sida 19: 264. 2000.

*Pentachaeta group
Pentachaeta Nutt. [*Pentachaeta aurea*, *P exilis*]
Rigiopappus A. Gray [*Rigiopappus leptocladus*] Monotypic.
Tracyina S.F. Blake [*Tracyina rostrata*] Monotypic.

*Ericameria group
Ericameria Nutt. [many species; see Roberts & Urbatsch 2003]

Morphological differences between the *Pentachaeta* group (mostly annual herbs) and the *Ericameria* group (shrubs) are striking and each might reasonably be treated at subtribal rank. Molecular data indicate that they have a sister relationship and together are distant from other genera.

14. SOLIDAGININAE O. Hoffm. in Engler & Prantl, Nat. Pflanzenf. 4(5): 145. 1890.

*Unresolved genera (ambiguous placement in molecular phylogenies)
Eastwoodia Brandeg. [*Eastwoodia elegans*] Monotypic.
Columbiadoria Nesom [*Columbiadoria hallii*] Monotypic.

*Sericocarpus group
Sericocarpus Nees [*Sericocarpus asteroides*, *S. linifolia*, *S. oregonensis*, *S. tortifolius*]

*Cuniculotinus group
Cuniculotinus Urbatsch, Roberts, & Neubig [*Cuniculotinus gramineus*] Monotypic.

*Chrysothamnus group
Acamptopappus (A. Gray) A. Gray [*Acamptopappus shockleyi*, *A. sphaerocephala*]
Amphipappus Torr. & Gray ex A. Gray [*Amphipappus fremontii*] Monotypic, 2 varieties.
Chrysothamnus Nutt. [*Chrysothamnus depressus*, *C. eremobius*, *C. greenei*, *C. humilis*, *C. molestus*, *C. stylosus*, *C. vaseyi*, *C. viscidiflorus*]

*Solidago group
Bathysanthus Nesom Monotypic, southern Chihuahua (Nesom 2018a). No molecular sample.
Brintonia Greene [*Brintonia discoidea*]
Oligoneuron Small [*Oligoneuron nitidum*, *O. rigidum*]
Solidago L. [*Solidago bicolor*, *S. canadensis*, *S. fistulosa*, *S. patula*, *S. petiolaris*, *S. sempervirens*, *S. shortii*]
Chrysoma Nutt. [*Chrysoma pauciflosculosa*] Monotypic.

*Stenotus group
Nestotus Roberts, Urbatsch, & Neubig Genus of 3 species (Nesom 2018b). *Nestotus lanuginosus*, *N. macleanii*, *N. stenophyllus*).
Oreochrysum Rydb. [*Oreochrysum parryi*] Monotypic.
Tonestus A. Nels. Genus of 2 species. [*Tonestus lyallii*, *T. pygmaeus*].
Lorandersonia Urbatsch, Roberts, & Neubig [*Lorandersonia baileyi*, *L. linifolia*, *L. microcephala*, *L. pulchella*, *L. salicina*] The genus also includes a sixth species, *Lorandersonia spathulata*.
Stenotus Nutt. Genus of 3 species (Nesom 2018b). [*Stenotus acaulis*, *S. armerioides*, *S. pulvinatus*].
Toiyabea Roberts, Urbatsch, & Neubig Four species of California and Nevada. *Toiyabea alpina*, *T. eximia*, *T. granitica*, *T. peirsonii*. See Nesom (2020a) for taxonomy that contradicts molecular data.
Petradoria Greene [*Petradoria pumila*] Monotypic.

15. SYMPHYOTRICHINAE Nesom, Phytologia 76: 211. 1994.
Sanrobertia Nesom [*Sanrobertia gypsophila*] Monotypic.
Canadanthus Nesom [*Canadanthus modestus*] Monotypic.
Ampelaster Nesom [*Ampelaster carolinianus*] Monotypic.
Almutaster Löve & Löve [*Almutaster pauciflorus*] Monotypic.
Psilactis A. Gray [*Psilactis asteroides*, *P. boltoniae*, *P. brevilingulata*, *P. odysseus*, *P. tenuis*]
Symphyotrichum Nees [many species, incl. *Symphyotrichum chapmanii*, *S. ciliatum*, *S. cordifolium*, *S. dumosum*, *S. ericoides*, *S. moranense*, *S. sericeum*, *S. subulatum*, *S. turbinellum*]

SOUTH AMERICA

16. BACCHARIDINAE Less., Linnaea 5: 145. 1830.

*Baccharis group
Baccharis L. (syns = *Baccharidastrum*, *Baccharidiopsis*, *Heterothalamulopsis*, *Heterothalamus*, *Heterothalamulopsis*, *Lanugothamnus*, *Molina*, *Neomolina*, *Pingraea*, *Pseudobaccharis*, *Psila*, *Sergilus*, *Stephananthus*, *Tursenia*; see Heiden et al. 2019)

The phylogenetic position of *Baccharis* is ambiguous but most indications (e.g., Vargas et al. 2017) are that it arose from among species previously treated as Hinterhuberinae, with *Aztecaster*, *Archibaccharis*, *Parastrephia*, and species of *Diplostephium* sensu lato among its closest woody relatives.
Exostigma Sancho [*Exostigma notobellidiastrum*]

The position of *Exostigma* is not resolved; several molecular analyses place it as most closely related to *Baccharis*, with which it seems to have little in common morphologically.

*Hinterhubera group (Hinterhuberinae Cuatr., Webbia 24: 5. 1969)
Blakiella Cuatr. [*Blakiella bartsiifolia*] Monotypic.
Flosmutisia Cuatr. Monotypic. Not included in molecular sampling.
Flosmutisia paramicola is distinctive in its rosulate habit, solitary heads, multiseriate rays, subbiliabiate ray corollas, and functionally male disc flowers. Cuatrecasas (1986) noted that its probable closest relatives are *Hinterhubera*, *Blakiella*, and *Westoniella*.
Hinterhubera Sch.-Bip. ex Wedd. [*Hinterhubera adenopetala*, *H. columbica*, *H. ericoides*, *H. imbricata*, *H. lanuginosa*, *H. laseguei*]
Laestadia Kunth ex Less. [*Laestadia costaricensis*, *L. muscicola*, *L. pinifolia*]

*Linochilus group
Linochilus Benth. (segregated from *Diplostephium*) [many species sampled; see Vargas 2018 and Saldivia et al. 2019]

*Laennecia group
Laennecia Cass. [*Laennecia schiedeana*, *L. sophiifolia*]
Talamancaster Pruski (segregated from *Lagenophora*; Pruski 2017) [*Talamancaster cuchumatanica*, *T. panamensis*]
Westoniella Cuatr. [*Westoniella chirripoensis*, *W. eriocephala*, *W. kohkemperi*, *W. triunguifolia*]

*Aztecaster group
Aztecaster Nesom [*Aztecaster matudae*, *A. pyramidatus*]

*Archibaccharis group
Archibaccharis Heering [*Archibaccharis androgyna*, *A. asperifolia*, *A. schiedeana*]
Plagiocheilus Arn. ex DC. [*Plagiocheilus bogotensis*, *P. soliviformis*]

*Diplostephium group
Diplostephium Kunth sensu stricto [incl. *Dysaster* H. Rob. & Funk = *Diplostephium serratifolium*; many species sampled; see Vargas 2018]
Floscaldasia Cuatr. [*Floscaldasia hypsophila*]
Parastrephia Nutt. [*Parastrephia lepidophylla, P. lucida*, *P. phylicaeformis*, *P. quadrangularis*, P. *teretiuscula*]

*Pacifigeron group
Guynesomia Bonif. [*Guynesomia scoparia*] Monotypic.
Kieslingia Faúndez, Saldivia, & Martic. [*Kieslingia chilensis*] Monotypic.
Pacifigeron Nesom [*Pacifigeron indivisus, P. rapensis*]
Genus of 2 species from the island of Rapa in French Polynesia; see Saldivia et al. (2020).

*Podocoma group (Podocominae Nesom, Phytologia 76: 209. 1994)
Podocoma itself is perhaps separate from the others.
Asteropsis Less. [*Asteropsis megapotamica*] Monotypic.
Inulopsis (DC.) O. Hoffm. [*Inulopsis scaposa*]
Microgyne Less. [*Microgyne marchesiana*, *M. trifurcata*]
Podocoma Cass. [*Podocoma asperrima*, *P. hieracifolia*, *P. hirsuta*]
Sommerfeltia Less. [*Sommerfeltia cabrerae*, *S. spinulosa*]

17. CHILIOTRICHINAE Bonifacino, **subtr. nov.** **TYPE**: *Chiliotrichum* Phil.
Contributed by Mauricio Bonifacino

Shrubs (usually densely branched) or small scandent trees; leaves coriaceous, usually reduced and ericoid (except in *Llerasia*) and usually densely tomentose abaxially; receptacles paleate or partially paleate (rarely epaleate; i.e., *Llerasia*, *Ocyroe*); ploidy level 2x or 4x. Mostly Andean South America. See analysis by Bonifacino and Funk (2012).

Aylacophora Cabrera [*Aylacophora deserticola*] Monotypic.
Cabreraea Bonif. [*Cabreraea andina*] Monotypic.
Chiliophyllum Phil. [*Chiliophyllum densifolium*]
Chiliotrichiopsis Cabrera [*Chiliotrichiopsis keidelii*, *C. ledifolia*, *C. peruviana*]
Chiliotrichum Cass. [*Chiliotrichum diffusum*, *C. fuegianum*]
Haroldia Bonif. [*Haroldia mendocina*] Monotypic.
Katinasia Bonif. [*Katinasia cabrerae*] Monotypic.
Lepidophyllum Cass. [*Lepidophyllum cupressiforme*]
Llerasia Triana [*Llerasia lindenii*, *L. lucidula*, *L. ledifolia*, *L. rufescens*, *L. soratensis*]
Nardophyllum (Hook. & Arn.) Hook. & Arn. (incl. *Paleaepappus* Cabr.) [*Nardophyllum bryoides*, *N. lanatum*, *N. chiliotrichioides*, *N. genistoides*, *N. patagonicum*]
Ocyroe Phil. [*Ocyroe armata*] Monotypic.

18. ORITROPHIINAE Nesom, **subtr. nov.** **TYPE**: *Oritrophium* (Kunth) Cuatr.

Related to Chiliotrichinae but distinct in its combination of herbaceous habit, narrow, 1-veined or parallel-veined leaves in basal rosettes, leaf axils with tufts of hairs, epaleate receptacles, disc flowers with sterile ovaries, blunt anther thecae bases, and multinerved achenes with persistent pappus bristles; ploidy level 2x or 4x.

Novenia Freire [*Novenia acaulis*]
Oritrophium (Kunth) Cuatr. [*Oritrophium hieracioides, O. peruvianum*]

OCEANIA

19. LAGENOPHORINAE Nesom [as "Lageniferinae"], Phytologia 76: 207. 1994.

Keysseria Lauterb. (type = *Keysseria papuana* = *Keysseria radicans*). Including 9 species, all of alpine habitats in New Guinea (Koster 1966) and including considerable diversity in habit. Hawaian species previously treated as *Keysseria* are separated as *Helodeaster* (see Asterinae-Psychrogeton branch, the Myriactis group; Nesom 2020c).

Lagenocypsela Swenson & Bremer A single species, *Lagenocypsela* (*Rhamphogyne*) *papuana*.

Lagenophora Cass. (type = *Lagenophora stipitata*) [*Lagenophora barkeri*, *L. cuneata*, *L. gracilis*, *L. hariotii*, *L. hirsuta*, *L. huegelii*, *L. lanata*, *L. montana*, *L. nudicaulis*, *L. petiolata*, *L. pinnatifida*, *L. pumila*, *L. stipitata*, *L. strangulata*]

Lagenophora gracilis and *L. huegelii* (Australia) and *L. lanata* (s and se Asia, Malaysia, New Guinea, Australia) are more closely related to *Solenogyne* than to the rest of *Lagenophora* (Nakamura et al. 2012; Sancho et al. 2015). Species of Australia and New Guinea are treated by Wang and Bean (2019, 2020).

Novaguinea D.J.N. Hind
Piora Koster A single species, *Piora ericoides*.
Pytinicarpa Nesom
Solenogyne Cass. (type = *Solenogyne bellioides*) [*Solenogyne gunnii*, *S. dominii*, *S. bellioides*, *S. mikadoi*] Also [*Lagenophora gracilis*, *L. lanata*, and *L. huegelii*], which apparently form part of *Solenogyne* rather than *Lagenophora*; see *Lagenophora*.

20. CELMISIINAE Saldivia, **subtr. nov.** **TYPE:** *Celmisia* Cass., Dict. Sci. Nat., ed. 2. 37: 259. 1825, nom. cons., non *Celmisia* Cass., Bull. Sci. Soc. Philom. Paris 1817: 32. 1817, nom. rej. (≡ *Capelio* B. Nord.). Contributed by Patricio Saldivia.

Small trees (rarely up to 18 m), erect or plagiotropic shrubs, subshrubs, or perennial herbs with large leaves; phyllotaxis alternate (2/5) or opposite, abaxial surface of the leaves covered by dense white to ferrugineous tomentum in most of the species (hairs long aseptate, T- or Y-shaped, or lepidote); shoots indeterminate with typically lateral flowering or plants with long shoots determinate by abortion rather than by floral development and short shoots (brachyblasts) bearing capitula and leaves; capitula radiate, or rarely disciform or discoid; capitulescences fasciculate, paniculate, corymbose or capitula solitary; ray flowers pistillate, occasionally with staminodes; disc flowers bisexual or functionally staminate (only in some *Olearia* pro parte species from New Guinea); anthers caudate and with a conspicuous apical appendage; receptacles epaleate, alveolate; achenes fusiform-cylindrical (mostly), obconic or gibbous, 4–13 ribbed, often covered with twin trichomes; ploidy level mainly 12x (but also 10x, 24x, 32x, 36x, and 48x; see Beuzenberg & Hair 1984). Ca. 159 species endemic to Australasia.

Celmisia Cass. [*Celmisia argentea*, *C. armstrongii*, *C. asteliifolia*, *C. bellidioides*, *C. glandulosa*, *C. holosericea*, *C. laricifolia*, *C. lateralis*, *C. longifolia*, *C. mackaui*, *C. tomentella*]

Ca. 60 species from mainland New Zealand (North, South, and Stewart islands), 6 species endemic to southeast mainland Australia, and 2 Tasmanian species. Biphyletic in Saldivia et al. (2020).

Damnamenia Given [*Damnamenia vernicosa*]

Monotypic, endemic to the sub-Antarctic Campbell and Auckland Islands of New Zealand.

Olearia Moench in part (84 species in total)

a. Macrocephalous *Olearia* species (6 species, New Zealand) [*Olearia angustifolia, O. chathamica*, *O. colensoi*, *O. lyallii*, *O. operina*, *O. semidentata*]

b. Sect. *Divaricaster* (13 species, New Zealand) [*Olearia fimbriata*, *O. solandri*, *O. traversiorum*, *O. virgata*] See Heads (1998) and Heenan et al. (2008).

c. New Zealand species with lepidote trichomes (8 species) [*Olearia albida*, *O. nummularia*, *O. paniculata*]

d. New Guinea species (19 species) [*O. rufa*, *O. velutina*]

e. Species with T- or Y-shaped trichomes and no divaricate architecture (except for the type species *Olearia tomentosa*), 14 species from New Zealand [*Olearia allomii*, *O. arborescens*, *O. cheesemanii*, *O. fragrantissima*, *O. furfuracea*, *O. rani*], 23 species from mainland Australia and Tasmania [*Olearia argophylla*, *O. chrysophylla*, *O. covenyi*, *O. ledifolia*, O. *megalophylla*, *O. myrsinoides*, *O. oppositifolia*, *O. pannosa*, *O. rosmarinifolia*], 1 species from Lord Howe Island [*Olearia mooneyi*].

Olearia species from Celmisiinae (formerly the *Celmisia* group) cannot be retained in *Olearia* since the type species, *O. tomentosa* from mainland Australia, belongs to a different lineage, Brachyscominae (see below and Saldivia et al. 2020). Molecular and morphological data (Cross et al. 2002; Wagstaff et al. 2011; Saldivia et al. 2020; Saldivia et al., unpublished data) indicate that the *Olearia* species from Celmisiinae need to be placed in two or more new genera.

Pachystegia Cheeseman [*Pachystegia insignis*, *P. rufa*] 3 species.

Pleurophyllum Hook. f. [*Pleurophyllum criniferum, P. hookeri, P. speciosum*]

3 species endemic to the sub-Antarctic New Zealand (Campbell, Auckland, and Antipodes) and Australian (Macquarie) islands.

21. BRACHYSCOMINAE Nesom, Phytologia 76: 203. 1994.

Annual to perennial herbs, subshrubs, and shrubs. Morphologically heterogeneous, suggested to be monophyletic by molecular analyses although many taxa have not been included in molecular

sampling. Almost all of the species are from Australia — the geography also supports a hypothesis of monophyly.

*Brachyscome group

Brachyscome Cass. (incl. *Allittia* P.S. Short, *Brachystephium* Less., *Paquerina* Cass., *Pembertonia* P.S. Short, *Roebuckia* P.S. Short, *Steiroglossa* DC.)

Chromosome numbers, 2*n* = 4, 6, 8, 10, 12, 14, 16, 18, 22, 24, 26, 27, 28, 30, 36.

For coments on the spelling of *Brachyscome* (vs. *Brachycome*), see Short (2014, pp. 27-28).

Ceratogyne Turcz.

Ceratogyne obionoides has not been included in molecular analyses but it previously has been placed in Astereae (Zhang & Bremer 1993; Nesom 1994a; Nesom & Robinson 2007). It is characterized by tiny heads with phyllaries in a single series, functionally staminate disc flowers, ray flowers with reduced ligules, and highly modified achenes (margins thickened and involute with glochidiate Zwillingshaare, arm-like, apically spreading wings, without pappus). Among Australian Astereae, its chromosome number of 2n = 12 (Turner 1970) occurs elsewhere only in *Brachyscome*, where it apparently has been independently derived several times (Field et al. 2006). "Given the diversity and parallel variability that exists within *Brachyscome* [e.g., Short 2014], it would not be surprising if *Ceratogyne* eventually proved to be a specialized derivative within some group of [*Brachyscome*]" (Nesom 1994a, p. 217). Features of *Ceratogyne* achene morphology approach those of species recently segregated as the genus *Roebuckia*, but the chromosome number of those species is consistently n = 9.

*Calotis group (both genera, x=8; Brachyscominae otherwise x=9 except for *Brachyscome* and *Ceratogyne*)

Calotis R. Br. [*Calotis anthemoides*, *C. cuneata*, *C. cymbacantha*, *C. dentex*, *C. erinacea*, *C. hispidula*, *C. inermis*, *C. lappulacea*, *C. latiuscula*, *C. multicaulis*, *C. plumulifera*, *C. porphyroglossa*, *C. scabiosifolia*, *C. scapigera*, *C. squamigera*, *C. xanthosioidea*]

Erodiophyllum F. Muell. [*Erodiophyllum elderi*]

*Vittadinia group

Peripleura (Burbidge) Nesom (except for *P. diffusa*)

Tetramolopium Nees (except for *T. vagans*)

Vittadinia A. Rich.

These genera together comprise a single clade but each apparently is polyphyletic (e.g., Lowrey et al. 2001). Current taxonomy does not accord with evolutionary patterns as reflected in molecular analyses.

*Elachanthus group

Chondropyxis D.A. Cooke [*Chondropyxis halophila*]

Elachanthus F. Muell. [*Elachanthus pusillus*]

Isoetopsis Turcz. [*Isoetopsis graminifolia*]

Kippistia F. Muell. [*Kippistia suaedifolia*]

Minuria DC. in part (type = *Minuria leptophylla*) [*Minuria cunninghamia*]

Minuria apparently is polyphyletic or else shows evidence of ancient gene flow; see below for *M. integerrima* and *M. macrorhiza*.

*unresolved

Achnophora F. Muell. [*Achnophora tatei*]

Camptacra Burbidge [*Camptacra barbata*, *C. gracilis*, and *C. robusta* (the latter identified in Cross et al. 2002 as *Olearia arguta*; see Bean 2020, Nesom 2020n)]

Dichromochlamys Dunlop [*Dichromochlamys dentata*]

Dimorphocoma Muell. & Tate

Hullsia P.S. Short

Perennial herbs from a taproot, stems erect, distally branched; leaves cauline and evenly spaced, narrowly lanceolate, 3-nerved, glaucous and succulent, glabrous, eglandular; involucres 8–12 mm wide, phyllaries in 2–3 series of subequal length; disc florets functionally staminate, corollas 5-lobed; ray corollas with prominent, coiling ligules; achenes 2.7–3.1 mm long, flattened, 2-nerved, glabrous, carpododium annular; pappus absent. *Hullsia argillicola*, northern Australia. Short (2004b) considered possible relatives in Brachyscominae and Lagenophorinae but found *Hullsia* isolated; its placement here seems more likely than in Lagenophorinae.

Iotasperma Nesom

Ixiochlamys Sond. [*Ixiochlamys cuneifolia*, *I. filicifolia*]

Minuria DC. in part [*Minuria macrorhiza*, related to *Peripleura diffusa*; *M. integerrima*, suggest by molecular data as related to *Walsholaria*.

Pappochroma Raf. [*Pappochroma nitidum*]

Pilbara Lander

Monotypic genus endemic to the Pilbara region of Western Australia. Highly branched shrubs up to 60 cm tall, with exfoliating, fissured, and fibrous bark; leaves tightly clustered distally, petiolate, coarsely and irregularly serrate, stipitate-glandular; heads few, discoid; phyllaries herbaceous; receptacles strongly convex, paleate; disc corollas white, tube filiform, abruptly opening into the limb; anther bases obtuse; achenes ellipsoid, 3.3–4.6 mm long, 5-ribbed; pappus 1-seriate, of barbellate bristles half as long as the corollas.

Lander (2013) compared *Pilbara* to *Erodiophyllum* but the two seem to have little in common except for paleate receptacles. It seems likely that *Pilbara* is more evolutionarily isolated than tentatively placed here.

Remya Hillebr. ex Benth. & Hook. f. [*Remya kauiensis*, R. *mauiensis*]

Three species in Hawaii. The only genus of Brachysominae without Australian species.

*<u>*Olearia* Moench sensu stricto</u> ("clade A" of Cross et al. 2002)

After segregation of *Olearia* species of subtr. Celmisiinae (all of which eventually will be transferred to other genera — but see comments below on *Olearia tomentosa*), and after recognition of recently segregated genera (Nesom 2020n), the genus comprises three groups essentially restricted to Tasmania and the Australian mainland. Sect. *Asterotriche* is monophyletic, while the taxonomic status of various subgroups of sect. *Eriotriche* (Nesom 2020n) remains to be resolved. It seems likely that "clade A" sect. *Eriotriche* (as a whole or in parts) and sect. *Asterotriche* will be recognized at generic rank apart from *Olearia*. The placement of *Olearia tomentosa* (the type of the genus, with "T-shaped" hairs, sect. *Dicerotriche*) as distantly related to other Australian species with similar hairs (but all unequivocally placed in Celmisiinae although apparently not forming a monophyletic group) is surprising — morphological evidence supporting a hypothesis of evolutionary parallelism in *O. tomentosa* is discussed by Saldivia et al. (2020) and Messina et al. (2014). Circumscription of *Olearia* in the strictest sense and its evolutionary position are unsettled but it seems possible that the genus *Olearia* eventually may be recognized as monotypic, sister to the Australian sect. *Asterotriche* species.

sect. *Olearia* (formerly sect. *Dicerotriche*) [*O. tomentosa*]

sect. *Asterotriche* [*O. asterotricha*, *O. astroloba*, *O. brevipedunculata*, *O. canescens*, *O. frostii*, *O. gravis*, *O. heterocarpa*, *O. hygrophila*, *O. lasiophylla*, *O. lirata*, *O. montana*, *O. nernstii*, *O. phlogopappa*, *O. quercifolia*, *O. rugosa*, *O. stellulata*, *O. stenophylla*, *O. viscidula*]

sect. *Eriotriche* [*O. algida, O. ballii*, *O. floribunda*, *O. microphylla*, *O. passerinoides*, *O. pimeleoides*, *O. ramosissima*, *O. ramulosa*, *O. teretifolia*] See Nesom (2020n) for subgroups of sect. *Eriotriche*.

*<u>unresolved</u> — <u>Olearia segregates</u> (Nesom 2020n)

Landerolaria Nesom [*Landerolaria stuartii*] 10 species.

Neolaria Nesom [*Neolaria ferresii*] 3 species.

Phaseolaria Nesom [*Phaseolaria elliptica*] 3 species.

Walsholaria Nesom [*Walsholaria calcarea*, *W. muelleri*] 4 species.
Muellerolaria Nesom [*Muellerolaria rudis*, *M. picridifolia*] 2 species.
Eoglandula Nesom [*Eoglandulosa glandulosa*] 2 species.
Linealia Nesom [*Linealia floctoniae*] Monotypic.
Vicinia Nesom [*Vicinia ciliata*] 2 species.
Wollemiaster Nesom [*Wollemiaster cordatus*] Monotypic.
Ephedrides Nesom *Ephedrides trifurcata*, not included in molecular sampling. Monotypic.

EURASIA

22. ASTERINAE (Cass.) Dumort., Fl. Belg. Prodr. 66. 1827.

A. ASTERINAE-PSYCHROGETON branch

*Psychrogeton group

Neobrachyactis Brouillet (*Neobrachyactis roylei*-the type) [*Neobrachyactis obovatus*, *N. roylei*] [*Psychrogeton pseudoerigeron*]

In contrast to the other species of *Neobrachyactis*, *N. anomala* (DC.) Brouillet is perennial and does not have accrescent pappus bristles — features that are more like *Psychrogeton*. The taxonomy and evolutionary position of *Neobrachyactis* remain to be clarified.

Psychrogeton Boiss. (excluding *Psychrogeton obovatus*, which was transferred to *Neobrachyactis* by Farhani et al. 2018) [*Psychrogeton aellenii*, *P. alexeenkoi*, *P. amorphoglossus*, *P. aucheri*, *P. cabulicus*, *P. chionophilus*, *P. nigromontanus*]

*Callistephus group

Callistephus Cass. [*Callistephus chinensis*]
Cordiofontis Nesom [*Cordiofontis* (Aster, Kalimeris) *longipetiolata*)

Cordiofontis longipetiolata (as *Kalimeris*) is included in the analyses of Li et al. (2012) and Farhani et al. (2018), based on the same sample; the voucher was collected in Sichuan, deposited at HNNU. *Cordiofontis* includes 4 other Himalayan species (Nesom 2020i).

*Albescentes group

Sinosidus Nesom [*Sinosidus* (Aster) *albescens*, *S. argyropholis*, *S. fulgidulus*, *S. lavanduliifolius*, *S. polius*]

Sinosidus includes 7 species (Nesom 2020m).

*Myriactis group

Helodeaster Nesom [*Helodeaster helenae*, *H. maviensis*]

Segregated from *Keysseria* (Nesom 2020c), including 3 species from Hawaii.

Myriactis Less. (type = *Myriactis nepalensis*) [*Myriactis humilis*, *M. nepalensis*, *M. wallichii*, *M. wightii*]

Metamyriactis Nesom [*Metamyriactis* (Aster) *pandurata*, *Aster auriculatus*, *M. pycnophylla*]

Metamyriactis includes 5 species (Nesom 2020g; *Aster auriculatus* is a synonym of *M. pandurata*).

*Batangensis group

Geothamnus Nesom [*Geothamnus* (Aster) *batangensis*] (Nesom 2020m).

*Asteroides group

Tibetiodes Nesom [*Tibetiodes* (Aster) *asteroides*, *T. brachytricha, T. diplostephioides*, *T. flaccida*, *T. salwinensis, T. setchuanensis*, *T. yunnanensis*]

Tibetiodes includes 27 species (Nesom 2020l).

*Fuscescens group
Griersonia Nesom [*Griersonia* (Aster) *fuscescens*, *G. senecionoides*]

Griersonia comprises 3 species, including one previously treated at varietal rank within *Aster fuscescens* (Nesom 2020m).

*Unresolved placement
Chlamydites J.R. Drummond (syn = *Wardaster* J. Small; *W. lanuginosus* = *Aster neolanuginosus* Brouillet et al.) No molecular sample: *Chlamydites prainii* (Nesom 2020h). Monotypic.

Iteroloba Nesom No molecular sample: *Iteroloba* (Aster) *bipinnatisecta* (Nesom 2020m) Monotypic.

B. ASTERINAE-HERSILEOIDES branch

Yonglingia Nesom [*Yonglingia* (Aster) *hersileoides*; *Y. nitida*]

The 2 species of *Yonglingia* (Nesom 2020f) together appear in molecular analyses as basal (sister) to the Aster/Asterothamnus branches of Asterinae.

C. ASTERINAE-ASTEROTHAMNUS branch

*Asterothamnus group
Arctogeron DC. [*Arctogeron gramineus*]
Asterothamnus Novopokr. [*Asterothamnus centraliasiaticus*, *Asterothamnus fruticosus*]
Kemulariella Tamamsch. Placed here by morphology and geography.
Rhinactinidia Novopokr. (syn = *Krylovia* Schischk.) [*Rhinactinidia eremophila*, *R. limoniifolia* (= *Aster lingii*)]

The analysis of Li et al. (2012) places *Aster eremophilus* and *A. limoniifolius* (of *Rhinactinidia*) in close relationship to *A. amellus*. Koryluk et al. (2015), using the Li et al. samples, place them similarly — using new samples, however, their analysis places *Rhinactinidia* as closely related to *Asterothamnus*, a hypothesis adopted here, favored by morphology, geography, and ecology (see Korolyuk (1997, 1999; fide Korolyuk et al. 2015) for morphological support for monophyly of *Arctogeron*, *Asterothamnus*, *Kemulariella*, and *Rhinactinidia*).

Sinobouffordia Nesom [*Sinobouffordia* (Aster) *poliothamnus*, *S. sikuensis*] (Nesom 2020f).
Chaochienchangia Nesom [*Changchaochienia* (Aster) *falcifolia*] (Nesom 2020f).

*Cardiagyris group
Cardiagyris Nesom (the *Aster scaber* group) [*Cardiagyris dimorphophylla* = *Aster dimorphophyllus*; *C. komonoensis*, *C. japonica* (as *Aster miquelianus*), *C. rugulosa*, *C. scabra*; *C. dolichophylla*, *C. huangpingensis*]

Molecular data place *Cardiagyris* (9 species) as sister to the *Asterothamnus* group. (Nesom 2020j).

D. ASTERINAE-ASTER branch

*Sinoangustifolius group
Aster sinoangustifolius Brouillet et al. (replacement name for *Aster angustifolius* C.C. Chang). [*Aster sinoangustifolius*]

This species is sister to the *Aster amellus*/*Kalimeris* combined group. It has been placed in *Kalimeris* and *Miyamayomena* and seems morphologically closest to the latter.

*Amellus group
Aster L. sensu stricto [*Aster amellus*; *Aster alpinus*] See Nesom (2020e).

Aster, unplaced species [*A. maackii*; *A. procerus*; *A. pseudosimplex*; *A. sampsonii*; *A. taiwanensis*; *A. taliangshanensis*; *A. tataricus*; *A. tenuicaulis*; *A. tianmenshanensis*; *A. tonglingensis*; *A. viscidulus*] [*Aster baccharoides*; *A. jishouensis*; *A. turbinatus*]
Rhynchospermum Reinw. [*Aster verticillatus*]
Miyamayomena Kitam. sensu stricto [*Aster piccolii*, *A. pseudosimplex, A. simplex* (China), *A. savatieri* (Japan-Korea). *Miyamayomena koraiensis* (= *Aster koraiensis*) clusters with the Kalimeris group. The position of *A. savatieri* (the type) is ambiguous.
Turczaninovia DC. [*Turczaninovia fastigiata* = *Aster fastigiatus*]

*Kalimeris group
Kalimeris (Cass.) Cass. [*Aster incisus*, *A. indicus*, *A. integrifolius*, *A. pekinensis*, *A. pinnatifidus*, *A. yomena*]
Heteropappus Less. [*Aster altaicus*, *A. asagrayi*, *A. crenatifolius*, *A. hispidus*, *A. kantoensis*]
Aster sect. *Ageratoides* (Kitam.) Nesom sensu stricto [*Aster ageratoides* var. *lasiocladus, A. oliganthus*, *A. saxicola*]
Aster, sect. *Ageratoides* clade [*A. leiophyllus*, *A. myendorfii*, *A. oharai*, *A. pseudoglehnii*, *A. semiamplexicaulis*, *A. shusanensis*, *A. spathulifolius*]
Aster, sect. *Ageratoides* clade [*A. fanjingshanicus*]
Aster, sect. *Ageratoides* clade [*A. brevicaulis*, *A. dianchuanensis*, *A. handelii*, *A. homochlamydeus*, *A. tongolensis*]
Aster, sect. *Ageratoides* clade [*A. heterolepis*, *A. smithianus*]
Aster, sect. *Ageratoides* clade [*A. dolichopodus*, *A. mangshanensis*, *A. oreophilus*]
Aster, sect. *Ageratoides* clade [*A. souliei*]
Aster, sect. *Ageratoides* clade [*A. vestitus*]
Miyamayomena Kitam. in part [*M. koraiensis* = *Aster koraiensis*, placed in the Kalimeris clade fide Shin et al. 2014 and Jafari et al. 2015], apparently closely related to *A. spathulifolius*.
Sheareria S. Moore [*Sheareria nana*]

23. BELLIDINAE Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 30. 1870.
*Bellis group
Bellis L.
Bellium L.
Bellidiastrum Scop.

See analyses in Fiz-Palacios et al. (2002), including many species of Bellidinae.

*Galatella group
Galatella (Cass.) Cass. [*Galatella altaica*, *G. angustissima*, *G. biflora*, *G. dahurica*, *G. divaricata*, *G. dracunculoides*, *G. hauptii*, *G. litvinovii*, *G. scoparia*, *G. tatarica*, *G. villosa*]
Crinitina Soják [*Crinitina linosyris*]
Tripolium Nees [*Tripolium vulgare* = *Tripolium pannonicum*]

Relationships among species of the *Galatella* group are unresolved, but analyses of Farhani et al. (2018) and others suggest that *Tripolium* and *Galatella* are reasonably treated as distinct, with *Crinitina* included in the latter.

*Kitamuria group
Kitamuria Nesom [*Kitamuria glehnii* = *Aster glehnii*]
Monotypic genus, endemic to Japan, Sakhalin, and the Kuriles (Nesom 2020d).

Relationships among the three Bellidinae groups are unresolved by molecular data but the subtribe as summarized here is indicated to be monophyletic (Brouillet et al. 2009). Morphological similarities exist

between *Kitamuria* and the Galatella group (Nesom 2020d) but as a pair they are distant from the Bellis group.

24. CHAMAEGERINAE Nesom, **subtr. nov. TYPE**: *Chamaegeron* Schrenk

Annual or biennial herbs, taprooted, stipitate-glandular; heads relatively small (except *L. gossypinum*), in loose panicles; ray flowers 1–2-seriate, ligules white to blue, pink, or violet, coiling; disc flowers bisexual, fertile; achenes glabrous to sericeous-villous, eglandular; pappus bristles 1-seriate, connate in basal ring and basally caducous as a unit.

Chamaegeron Schrenk [*Chamaegeron asterellus*, *C. bungei*, *C. keredjensis*, *C. oligocephalus*]
Lachnophyllum Bunge [*Lachnophyllum gossypinum*, *L. noaeanum*]

The two species of *Lachnophyllum* are highly distinct from each other in morphology — *L. noaeanum* is similar to *Chamaegeron* in its short vestiture and relatively small heads in a loose panicle, while *L. gossypinum* (the type) is cobwebby-sericeous and produces fewer and larger heads with longer and broader rays. The nrDNA ITS data of Jafari et al. (2015) placed *L. gossypinum* with *Chamaegeron*. In the analyses of Farhani et al. (2018), nuclear DNA (ITS+ETS) data place both *Lachnophyllum* species with *Chamaegeron*, while plastid DNA *trn*L-F data place *L. noaeanum* with *Chamaegeron* but *L. gossypinum* within the Callistephinae, suggesting that its genome has been influenced by ancient hybridization/ introgression events.

25. FORMANIINAE Nesom, **subtr. nov. TYPE**: *Formania* W. Smith & J. Small

Sprawling shrubs, stems 30–100 cm long; leaves alternate, thickened, margins shallowly lobed to coarsely and irregularly serrate with spinulose teeth, surfaces minutely stipitate glandular in pits and viscid. heads terminal in loose corymbs; involucres cylindric; phyllaries in 4 strongly graduate series, scarious, stipitate-glandular and resinous, with a green apical patch; receptacles fimbrillate, epaleate; ray flowers ca. 10, ligules 2.5–3 mm long, pale yellow; disc flowers ca. 8, bisexual, corolla lobes 5, triangular; anther bases sagittate with a short, acute auricle at base, apical appendages long acute; style branch tips lanceolate; achenes obovoid, 3-ribbed, strigose and sparsely stipitate glandular; pappus of 5–6 linear, acute-tipped pales and a shorter series of bristles. Dry rocky slopes and rock faces; western Sichuan and northwest Yunnan.

[*Formania mekongensis*]

The molecular analysis of Fu et al. (2016) places *Formania* in a clade with *Dichrocephala benthamii* and *Aster flaccidus* (Asterinae). Their sampling, however, was sparse and *Callistephus chinensis* (Asterinae) does not cluster with the *Formania* group. The position of *Formania* within the Astereae is secure but other inferences are not justified on the basis of the Fu et al. analysis. The phylogenetic positioning (Fig. 1) of *Formania* is speculative.

Formania resembles some species of Grangeinae in its tendency for glandular, lobed leaves and glandular achenes but it is distinct from all in its combination of a shrubby habit, campanulate involucres with scarious phyllaries in 4–5 graduate series, broad, yellow rays, bisexual disc flowers, tailed anther bases, and pappose achenes. It has little in common with the *Psiadia* group of Grangeinae.

Brouillet et al. (2009) reckoned that tailed anther bases are primitive in Astereae. As noted here, they occur in *Printzia* and *Denekia*, Chiliotrichinae and Celmisiinae, Mairiinae, and Madagasterinae — their presence in *Formania* suggests that it also is a primitive element in the tribe.

26. IRANOASTERINAE Nesom, **subtr. nov. TYPE**: *Iranoaster* Kaz.-Osaloo

Perennial herbs from a thick, woody taproot; stems 5–20 cm tall, mostly unbranched except near the base; leaves all cauline, evenly spaced up to the heads, sessile to short-petiolate, 1–1.5 cm long, lowermost cauline scale-like; heads solitary, involucres ca. 15 mm wide, phyllaries in 3–5 strongly graduate series; ray flowers 10–16, ligules purple to whitish-pink, coiling; achenes ca. 2.5 mm long, linear to obovate, sericeous; pappus bristles 1-seriate, apically attenuate.

Iranoaster Kaz.-Osaloo, Farhani, & Mozaff.

Including a single species, *Iranoaster* (Aster) *bachtiaricus*, from the Zagros Mountains of Iran. A line drawing is part of the species protologue (Mozaffarian 1996; image of type collection not available; holotype, TARI). This species apparently is basal to a large part of the Astereae (Farhani et al. 2018).

27. NANNOGLOTTIDINAE Nesom, **subtr. nov. TYPE**: *Nannoglottis* Maxim.

Subshrubs (*N. ravida*) or perennial herbs, stipitate-glandular; basal leaves large, petiolate, margins evenly sharp-dentate, cauline leaves reduced, sessile, decurrent to clasping; heads relatively large, solitary (*N. ravida*) or loosely corymboid; flowers trimorphic — rays pistillate, yellow; inner pistillate in several series, eradiate; disc flowers functionally staminate, lobes deeply cut, reflexing-coiling, anther thecae without tails; fertile achenes subterete, 8–10-ribbed, eglandular; pappus of barbellate bristles in 1 series.

Nannoglottis Maxim. [8 species sampled; see analysis by Liu et al. 2002]

Nannoglottis includes 9 species endemic to the Tibetan Plateau of central Asia. *Nannoglottis ravida*, a subshrub of alpine habitas, comprises the sister clade to the others, which are perennial herbs of the coniferous forest (Liu et al. 2002). Liu et al. suggested that, because the Astereae apparently originated in the Southern Hemisphere, the best explanation for origin of *Nannoglottis* is "a long dispersal using Southeast Asia as a stepping-stone."

AFRICA/ MADAGASCAR/ SE ASIA

28. AFROASTERINAE Nesom, **subtr. nov. TYPE**: *Afroaster* Manning & Goldblatt

Perennial herbs from tuberous roots; basalmost leaves scale-like, cauline mostly on proximal 1/3–2/3 of stem, narrow and elongate, parallel-veined, hispid to glabrous, eglandular; heads 1–10(–15) on ebracteate or few-bracteate peduncles; involucres campanulate, phyllaries in 3–4 graduate to subequal series; ray flowers sometimes with staminodes, ligules white to blue or lilac, with a darker, abaxial midstripe, coiling; disc flowers bisexual, fertile; achenes narrowly elliptic to obovate, flat, mostly 2-nerved, often glandular or glandular and strigose-hirsute; pappus of 2 series of barbellate bristles, inner elongate, outer short.

Afroaster Manning & Goldblatt [*Afroaster comptonii*, *A. harveyanus*, *A. perfoliatus*]

Afroaster includes 18 species from Tanzania to South Africa (Eswatini, Lesotho, Malawi, Mozambique, South Africa, Tanzania, Transvaal, Zambia); revised by Lippert (1973) as *Aster*.

29. ESCHENBACHIINAE Nesom, **subtr. nov. TYPE**: *Eschenbachia* Moench

Annuals to perennial herbs or shrubs, taprooted or rhizomatous; leaves entire to serrate or pinnatifid, glandular or eglandular; heads discoid, in compact or loose clusters; outer florets pistillate, fertile, eligulate; disc florets fertile or with sterile ovaries; achenes 0.4–1.2 mm long, compressed, 2-nerved; pappus 1-seriate, bristles often accrescent, basally connate (typical) or free. Morphologically heterogeneous, indicated to be monophyletic by molecular analyses, badly needing taxonomic study.

Eschenbachia Moench (type = *Eschenbachia aegyptiaca* (L.) Brouillet = *Conyza aegyptica*)
[*Eschenbachia* (*Conyza*) *aegyptica*, *E.* (*C.*) *blinii*, *E.* (*C.*) *japonica*, *E.* (*C.*) *muliensis*, *E.* (*C.*) *gouanii*, *E.* (*C.*) *subscaposa*, *E.* (*C.*) *tigrensis*, *E.* (*C.*) *ulmifolia*]

Combinations above in *Eschenbachia* (species in molecular analyses) have been made by Brouillet (in Chen & Brouillet 2011) and Koster (1952) and are completed here:

Eschenbachia gouanii (L.) Nesom, **comb. nov.** *Erigeron gouanii* L., Mant. Pl. 469. 1771. *Conyza gouanii* (L.) Willd., Sp. Pl. 3: 1928. 1803.

Eschenbachia subscaposa (O. Hoffm.) Nesom, **comb. nov.** *Conyza subscaposa* O. Hoffm., Bot. Jahrb. Syst. 20: 225. 1894.

Eschenbachia tigrensis (Oliv. & Hiern.) Nesom, **comb. nov.** *Conyza tigrensis* Oliv. & Hiern., Fl. Trop. Afr. 3: 316. 1877.

Eschenbachia ulmifolia (Burm. f.) Nesom, **comb. nov.** *Baccharis ulmifolia* Burm. f., Fl. Indica 26. 1768. *Conyza ulmifolia* (Burm. f.) Kuntze, Revis. Gen. Pl. 3(3): 142. 1898.

Conyza L. in part (molecular analyses suggest that each of these three groups might be segregated at generic rank)

[*Conyza limosa*, *C. pinnata*]

[*Conyza attenuata*]

[*Conyza neocandolleana*]

Psiadia Jacq. ex Willd in part (see *Psiadia* sensu stricto in Grangeinae)

[*Psiadia amygdalina*, *P. anchusifolia*, *P. argentea*, *P. aspera*, *P. boivinii*, *P. callocephala*, *P. insignis*, *P. montana*, *P. laurifolia*, *P. reticulata*, *P. rivalsii*, *P. salaziana*, *P. sericea*]

Thespis DC. (lectotype = *Thespis divaricata*) [*Thespis divaricata*]

30. GRANGEINAE Benth. in Benth. & Hook., Gen. Pl. 2: 178. 1873.

Akeassia Lebrun & Stork

Ceruana Forssk.

Colobanthera Humbert

A single species from Madagascar; distinct among African Grangeinae in its functionally staminate disc flowers and broadly fusiform achenes, perhaps evolutionarily isolated and not part of this group.

Conyza Less. in part [*Conyza incisa*, *C. stricta*]

Dacryotrichia Wild

Dichrocephala L'Hér. ex DC. (*D. integrifolia*, the type) [*Dichrocephala benthamii*, *D. integrifolia*]

These two species are allied with *Grangea* in most analyses, but Farhani et al. 2018 place them with *Myriactis* and *Metamyriactis* based on ETS/ITS data, with *Grangea* based on based on plastid DNA. Fayed (1979) treated *Dichrocephala* among the genera of Grangeinae. The two species in the molecular sampling are similar to *Myriactis* in their Indian/southeast Asian geography (vs. African); the other two species of the genus (*D. chrysanthemifolia* and *D. alpina*) are primarily African in distribution, as with the rest of the subtribe. See Pruski (2011) for a summary of the genus.

Grangea Adans. [*Grangea maderaspatana*]

Grangeopsis Humbert

Grauanthus Fayed

Gyrodoma Wild

Heteromma Benth.

Mtonia Beentje

Nidorella Cass. [*Nidorella polycephala*, *N. resedifolia*]

Rhamphogyne S. Moore

A single species, *Rhamphogyne rhynchocarpa* S. Moore, endemic to Rodrigues.

*Psiadia group

Heteroplexis C.C. Chang

Species of *Heteroplexis* have not been included in molecular sampling but they are erect to climbing herbaceous perennials with small, few-flowered heads in terminal clusters, punctate-glandular leaves, ray corollas foreshortened or absent, and small achenes (ca. 1 mm long) — features similar to *Microglossa* and *Psiadia*. All five species are endemic to Guangxi, China, distinct in geography from the Southern Hemisphere-centered *Microglossa* and *Psiadia*.

Microglossa DC. (type = *M. volubilis*) [*Microglossa pyrifolia*] Molecular data suggest that the following should be be included within *Microglossa*:

Conyza Less. in part [*Conyza pyrrhopappa*, *C. scabrida*]

Psiadia in part [*Psiadia pascalii*]

Psiadia Jacq. ex Willd. sensu stricto (type = *Psiadia glutinosa*) [*Psiadia alticola*, *P. angustifolia*, *P. arguta*, *P. coarctata*, *P. coronopus*, *P. dentata*, *P. dimorpha*, *P. glutinosa*, *P. godotiana*, *P. leucophylla*, *P. melastomatoides*, *P. nigrescens*, *P. punctulata*, *P. serrata*, *P. viscosa*]
Psiadia sensu stricto also includes the following:
[*Sarcanthemum coronopus* = *Psiadia coronopus* (Lam.) Balf. f.]
[*Conyza ageratoides*]
[*Psiadiella humilis*]

The analysis of Strijk et al. (2013) indicates that *Conyza ageratoides* and *Psiadiella humilis* arose from within *Psiadia*.

Psiadia ageratoides (DC.) Nesom, **comb. nov.** *Conyza ageratoides*] DC., Prodr. 5: 385. 1836.
Other species of *Conyza* in Madagascar (at least those in Fig. L, p. 255, of Humbert 1960), probably also belong in *Psiadia*.

Psiadia humilis (Humbert) Nesom, **comb. nov.** *Psiadiella humilis* Humbert, Mém. Soc. Linn. Normandie 25: 39 (f. 1–10). 1923.

Welwitschiella Engler [*Welwitschiella nereifolia*]

Cyathocline Cass. (3 species, tropical Asia) was included within subtr. Grangeinae by Nesom and Robinson (2007) but evidence now shows that it is a member of tribe Inuleae (Li et al. 2014).

31. HOMOCHROMINAE Benth. in Benth. & Hook., Gen. Pl. 2: 174. 1873. **(**syn = Feliciinae Nesom)

*Amellus group
Amellus L. [*Amellus microglossus*, *A. strigosus*, *A. tridactylus*]
Chrysocoma L. [*Chrysocoma ciliata*]
Engleria O. Hoffm.
Felicia Cass. (type = *F. tenella*) *Felicia* is polyphyletic; see summary in Brouillet et al. 2009)
Sect. Felicia [*Felicia uliginosa*, F. *clavipilosa*] (these cluster with *Nolletia*)
Sect. Neodetris [*Felicia aethiopica*, *F. minima*, *F. namaquana*] (separate clade, sister to *Amellus*/*Polyarrhena*/*Zyrphelis*/*Felicia*
Sect. Anhebecarpaea [*Felicia echinata*] (with *Polyarrhena* and *Zyrphelis*)
Sect. Lignofelicia [*Felicia filifolia*, *F. fruticosa*, *F. linifolia*] (with *Polyarrhena* and *Zyrphelis*)
Gymnostephium Less.
Heteromma Benth.
Jeffreya Wild
Nolletia Cass. [*Nolletia chrysocomoides*]
Poeciliopsis Grau [*Poeciliopsis ficoidea*]
Polyarrhena Cass. [*Polyarrhena reflexa*]
Roodebergia B. Nord.
Zyrphelis Cass. (syn = *Homochroma* DC.) [*Zyrphelis decumbens*, *Z. microcephala*]

*Commidendron group
Commidendron Burch. ex DC. [*Commidendron rugosum*, *C. rotundifolium*, *C. robustum*, *C. spurium*]
Melanodendron DC. [*Melanodendron integrifolium*]

These two genera of trees, both endemic to island of Saint Helena, are evolutionary sisters — their ancestor apparently is a shrubby, *Felicia*-like species from the African mainland (Noyes & Rieseberg 1999; Eastwood et al. 2004).

32. MADAGASTERINAE Nesom, **subtr. nov. TYPE**: *Madagaster* Nesom

Subshrubs, shrubs, or small trees; leaves coriaceous, glabrous or abaxially tomentose, eglandular, venation camptodromous to brochidodromous; inflorescence terminal and 1-headed to corymboid; involucres cylindric (*Vernoniopsis*) or campanulate (*Madagaster*, *Rochonia*); receptacles epaleate; rays white to blue (*Madagaster*) yellow (*Rochonia*), or absent (*Vernoniopsis*); disc flowers bisexual, corolla lobes

triangular to linear-lanceolate; anther thecae bases caudate; achenes oblong-cylindric to fusiform, subterete, 4–10- nerved, eglandular; pappus of barbellate bristles. *Apodocephala* differs in its punctate-glandular leaves, paleate receptacles, deeply cut disc corolla lobes, and lack of pappus. Madagascar endemics.

Morphological similarities and geography support the hypothesis that *Apodocephala* (8 species; Humbert 1960), *Madagaster* (5 species; Nesom 1993), *Rochonia* (4 species; Humbert 1960), and *Vernoniopsis* (2 species; Callmander & Phillipson 2011) constitute a monophyletic group. *Madagaster* and *Rochonia* have radiate heads and campanulate involucres, while *Apodocephala* and *Vernoniopsis* are eradiate with cylindric involucres, but all species are trees or shrubs with coriaceous densely tomentose leaves (abaxially) and caudate anther thecae.

Madagaster Nesom [*Madagaster madagascariensis*, *M. mandrarensis*]
Rochonia DC.
Vernoniopsis Humbert

Apodocephala J. Baker

Shrubs or small trees; leaves coriaceous, abaxially tomentose, punctate-glandular, venation camptodromous to brochidodromous; inflorescence densely corymboid; involucres cylindric to campanulate; receptacles paleate; ray flowers absent; disc flowers few, corolla lobes narrowly lanceolate, cut to very base of limb; style branches strongly recurving-resupinate, collecting appendages ovate-deltate to linear-lanceolate, ca. 1/3–1/5 the length of the branches, branches internally papillate; anther thecae dark purplish, bases caudate, apical appendages white; achenes prismatic, 2–4-nerved, stipitate-glandular distally; pappus absent. 8 species, Madagascar.

Apodocephala was rejected as a member of Astereae by Nesom (1994a) and later unclaimed by any tribe, not included in a recent conspectus of the family (Kadereit & Jeffrey 2007). Humbert (1960), however, placed it as Astereae and given its overall similarity to the other Magasterinae genera, especially *Vernoniopsis*, probability is high that he was correct.

33. MAIRIINAE Nesom, **subtr. nov. TYPE**: *Mairia* Nees

Perennial herbs from woody rhizomes with succulent roots; stems scapose; leaves coriaceous to succulent or subsucculent, in a basal rosette, glandular or eglandular; heads 1 or less commonly 2–8, involucres mostly campanulate, 15–35 mm wide; phyllaries in 3–4(–6) weakly graduate series; receptacles epaleate; ray flowers with staminodes, ligules 3–5 mm wide, weakly coiling, white or pink to violet, staminodes nearly always present; disc flowers bisexual, thecae bases short-caudate, style branches with deltoid to triangular apical appendages; achenes narrowly fusiform to cylindric, (2–)4–7 nerved, punctate-glandular, sometimes strigose-sericeous; pappus 2-seriate, inner series of plumose bristles basally smooth or barbellate and coherent in a ring, outer series of long scales or reduced barbellate or plumose bristles.

Mairia Nees [*Mairia hirsuta*]

Mairia comprises 6 species (Herman & Zinnecker-Wiegand 2016), all endemic to coastal or near-coastal localities along the southern tip of South Africa.

34. PTERONIINAE Nesom, **subtr. nov. TYPE**: *Pteronia* L.

Evergreen shrubs, punctate-glandular or eglandular; leaves mostly opposite but sometimes alternate, linear to oblanceolate or ovate-oblong, often fleshy; heads discoid (ray flowers absent) on short peduncles, solitary or usually in corymbs; involucres campanulate to cylindric, phyllaries graduate and densely imbricate; receptacles epaleate; disc corollas usually yellow, sometimes white; style branches with deltate to triangular collecting appendages; anther thecae mostly obtuse at base; achenes often contracted at apex, villous to glabrous, glandular or eglandular; pappus bristles 2-seriate, barbellate, often basally connate or scale-like and broadened.

Pteronia L. [*Pteronia camphorata*, *P. uncinata*, *P. glomerata*, *P. incana*]

The genus comprises about 80 species (Bello et al. 2020) of southern Africa (Angola, Botswana, Lesotho, Namibia, South Africa, Swaziland, Zambia, Zimbabwe). The greatest concentration occurs in the Cape Floristic Region and the Succulent Karoo of South Africa and Namibia. Kolberg and Van Slageren (2014) recognized 24 species in Namibia.

35. PRINTZIINAE Nesom, **subtr. nov. TYPE**: *Printzia* Cass.

Shrubs; leaves coriaceous, tomentose abaxially; heads solitary on short peduncles; involucres cylindric; phyllaries 4–6-seriate, subequal; receptacle flat, epaleate; ray flowers 1-seriate, ligulate, purple or blue to white or yellowish, often coiled, rarely filiform, staminodes sometimes present; disc flowers bisexual, corollas yellow; anther thecae with long tails; style appendages lanceolate; achenes ellipsoid, mostly terete, multinerved, strigose, glandular; pappus of barbellate to subplumose bristles in 1–2 series.

Printzia Cass. [*Printzia polifolia*]

Six species, South Africa and LeSotho.

Printzia and *Denekia* are sister taxa in the analysis of Brouillet et al. (2009), at the very base of the Astereae. They are disparate in morphology (Figs. 4–12, below) — *Printzia* is generalized in morphology while *Denekia* is specialized. Species of both genera have tomentose abaxial leaf surfaces, tailed anthers, and subplumose to plumose pappus bristles, but otherwise their close common ancestry is hard to imagine.

Similarity in aspect of *Printzia* to *Rochonia*, *Madagaster* (Madagascar), *Diplostephium* (South America), and *Olearia* (Australia, New Zealand) suggests that features of these species are primitive for the tribe. As noted by Bayer and Cross (2002), in the protologue Cassini observed close similarities to *Olearia* and *Chiliotrichum* but *Printzia* differs from these in pollen type and style branch morphology

36. DENEKIINAE Nesom, **subtr. nov. TYPE**: *Denekia* Thunb.

Perennial herbs; leaves herbaceous, tomentose abaxially; heads in dense terminal clusters of few-20; involucres cupulate-campanulate; phyllaries 1(–2)-seriate; receptacle flat, epaleate; ray flowers with short 2-lobed ligules, blue or white, without staminodes; disc flowers with sterile ovaries, corollas blue or white; anther thecae with short tails; style appendages truncate; achenes ellipsoid, sparsely pilose, eglandular; pappus a single series of apically plumose bristles.

Denekia Thunb. [*Denekia capensis*]

One species, southern Africa (Angola, Botswana, Lesotho, Malawi, Mozambique, Namibia, South Africa, Swaziland, Tanzania, and Zimbabwe).

Figure 4. *Printzia pyrifolia*. South Africa. Photo by Cameron McMaster.

Figure 5. *Printzia pyrifolia*. Sitamani near Boston, South Africa. Photo by Peter R Warren, iNaturalist.

Figure 6. *Printzia pyrifolia*. Sitamani near Boston, South Africa. Photo by Peter R Warren, iNaturalist.

Figure 7. *Printzia pyrifolia*. Sitamani, South Africa. Photo by Christeen Grant (Life Wonderings of a Nature Lover.com site).

Figure 8. *Printzia auriculata*. Above the Mahai River, South Africa. Photo by Peter R. Warren, iSpot.

Figure 9. *Printzia aromatica* (above and below). Greyton Nature Reserve, South Africa. Photo by Klaus Wehrlin, iNaturalist.

Figure 10. *Denekia capensis*. Connemara Lake, Zimbabwe. Photo by M. Harvey-Hyde (Flora of Caprivi).

Figure 11. *Denekia capensis*. Spitskop Nature Reserve, South Africa. Photo by "JMK" on Wikipedia.

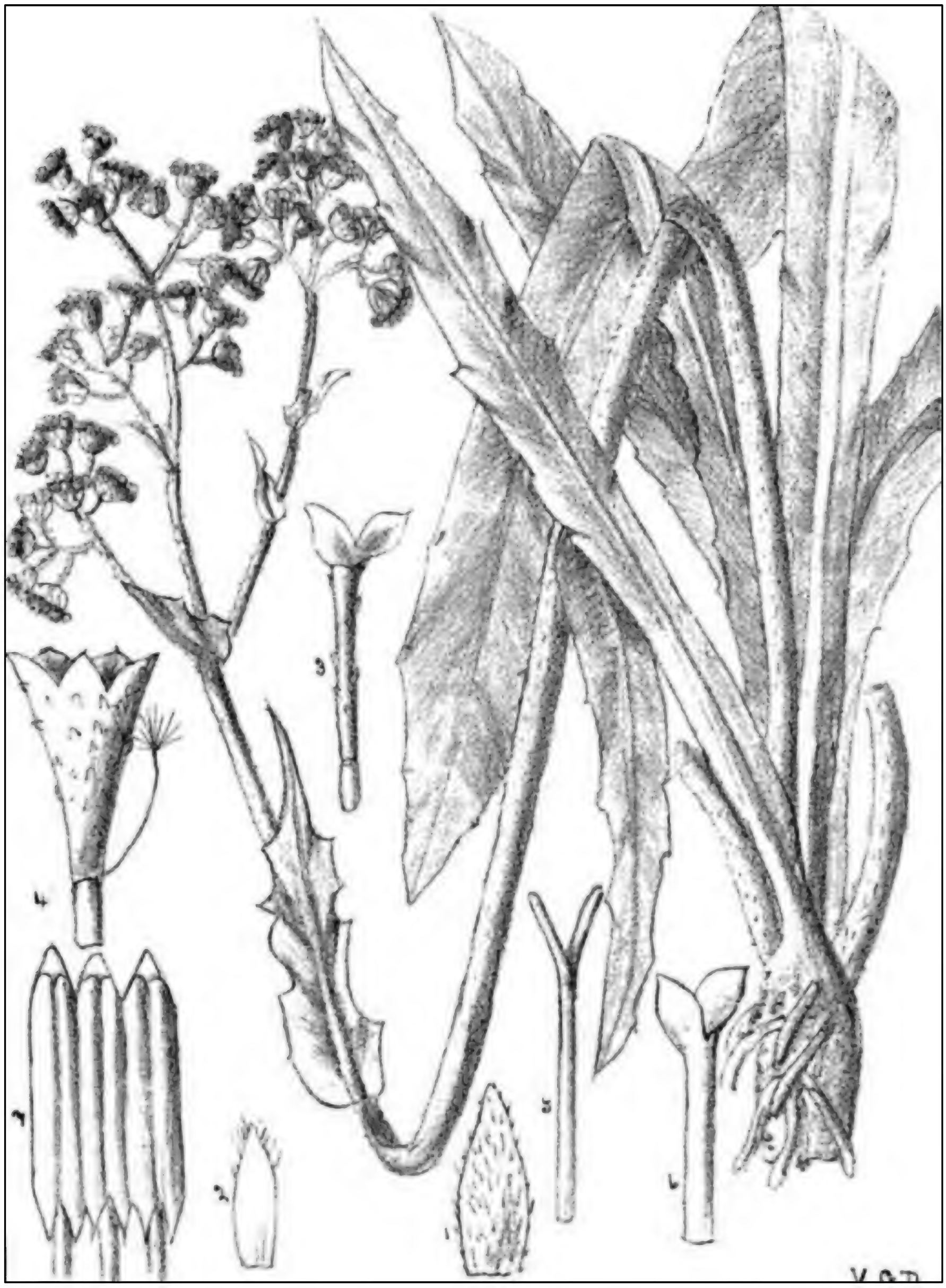

Figure 12. *Denekia capensis*. From J.M. Wood and M.S. Evans. 1898. Natal Plants: Descriptions and Figures of Natal Indigenous Plants. Natal Government and Durban Botanic Society.

Nesom, G.L. 2020. *Helodeaster*, a new genus for Hawaiian *Keysseria* (Asteraceae: Astereae). Phytoneuron 2020-54: 1–6.
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HELODEASTER, A NEW GENUS FOR HAWAIIAN *KEYSSERIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Keysseria in Hawaii (3 species) differs from putative congeners in Indonesia (9 species, including the type) in fertile disc flowers (vs. sterile in Indonesia) and achene morphology. In addition to the geographic disjunction, the Hawaiian plants are true to rainforest bogs, while the Indonesian ones are restricted to alpine habitats. Particularly because of the direction of evolution in the disc flowers, it is unlikely that the Hawaiian lineage is derived from the Indonesian one, and phylogenetic analyses based on molecular data indicate that the Hawaiian species are most closely related to *Myriactis* (subtr. Asterinae), of Australia, Indonesia, and southeast Asia. Hawaiian *Keysseria* are separated here as **Helodeaster** Nesom, **gen. nov. — *Helodeaster erici*** (Forbes) Nesom **comb. nov.**, ***Helodeaster helenae*** (Forbes & Lydgate) Nesom **comb. nov.**, and ***Helodeaster maviensis*** (H. Mann) Nesom **comb. nov.**

Keysseria Lauterb. comprises 12 species — 9 (including the type, *K. papuana*) in New Guinea; *K. radicans* also is known from Celebes and *K. gibbsiae* also occurs on Mt. Kinabalu in Borneo (Koster 1966). *Keysseria pickeringii* (A. Gray) Cabrera of Fiji was transferred to the genus *Pytinicarpa* (Nesom 2001). The transfer of three Hawaiian *Lagenophora* species into *Keysseria* (Cabrera 1967) introduced a significant discontinuity into the genus — the Hawaiian species have disc flowers with fertile ovaries (vs. sterile in Indonesia) and essentially beakless or short-beaked cypselae with a glandular apical collar (vs. with a distinct glandular neck or short beak). Based on morphology, Mill (1990) observed that the three Hawaiian species of *Keysseria* apparently are "from one founder," a hypothesis supported here.

In addition to a geographic disjunction of about 4500 miles from Indonesian *Keysseria*, the Hawaiian plants are true to rainforest bogs at 900–2000 meters, while the Indonesian ones are restricted to alpine habitats at (2400–)3100–4400 meters. "Rainfall in these [Hawaiian] localities varies from 200 to 600 inches per annum with some rain or fog practically every day of the year" (Forbes 1918).

Since Cabrera's transfer, the Hawaiian species have generally been recognized as *Keysseria* (e.g., St. John 1971; Carr 1985; HEAR 2020; USDA, NRCS 2020). Mill (1990), in contrast, maintained them in a broadly conceived *Lagenophora*, with *Keysseria* as a synonym. Swenson and Bremer (1994) also explicitly regarded *Keysseria* as a synonym of *Lagenophora*.

Central American species previously identified as *Lagenophora* have proved to be more closely related to American genera — they are now recognized as the genus *Talamancaster* (Pruski 2017) and placed in subtr. Baccharidinae (Nesom 2020). Hawaiian *Keysseria* are similar to *Talamancaster* in their laterally compressed and 2-ribbed, glandular-collared achenes and particularly to *T. sakiranus*, *T. minusculus*, and *T. andinus*, which have basal rosette and scapose stems.

DNA data, however, place Hawaiian *Keysseria* in close relationship to *Myriactis* Less. sensu stricto (e.g., Brouillet et al. 2009; Jafari et al. 2015). In the most recent complete and pertinent sampling and analysis (Farhani et al. 2018), *Myriactis* is placed as sister to *Dichrocephala* L'Hér. ex DC. (Grangeinae) based on plastid DNA but as most closely related to the genus *Metamyriactis* Nesom of China (Nesom 2020) based on ITS/ETS data. *Myriactis* and *Metamyriactis* are part of subtr. Asterinae.

Indonesian *Keysseria* species have not been sampled, but based on morphology and geography, they apparently belong with subtr. Lagenophorinae.

In summary, morphology points to a strong distinction between Hawaiian and Indonesian *Keysseria* and molecular data suggest that they have disparate evolutionary origins. It is improbable that the ancestral Hawaiian lineage would have reverted from sterile disc ovaries to fertile ones. Price and Wagner (2018) have provided numerous examples of Hawaiian taxa derived from those with a Australasian/Indo-Malayan/east Asian distribution, as is the case with Hawaiian *Keysseria*. The latter are treated here as a distinct genus.

HELODEASTER Nesom, **gen. nov.** **TYPE**: *Helodiaster maviensis* (H. Mann) Nesom
Keysseria sect. *Sandwicactis* Nesom, Sida 19: 514. 2001. **TYPE**: *Keysseria erici* (Forbes) Cabrera

Plants similar to Indonesian *Keysseria* in their perennial duration usually from a thickened rhizome, leaves thickened and in a basal rosette, solitary heads on scapose, bracteate stems, reduced ray corollas, laterally compressed, 2-ribbed achenes apically glandular but with glabrous to glabrate faces, and lack of pappus. Different from *Keysseria* sensu stricto in their disc flowers with fertile ovaries, disc corollas with 4–5 lobes, ray corollas often apically lobed, and achenes without a distinct neck or beak but with a glandular apical collar.

Helodeaster erici (Forbes) Nesom, **comb. nov.** *Lagenophora erici* Forbes, Occas. Pap. Bishop Mus. Honolulu 6: 60. 1918. *Keysseria erici* (Forbes) Cabrera, Blumea 14: 307. 1967. **TYPE: Hawaii**. **Kauai**. Waimea drainage, west side, Alakai swamp, in cushion of sedge, 3 Jul-18 Aug 1917, *C.N. Forbes 882K* (holotype: BISH?; isotype: NY image). The NY sheet is a duplicate distributed from BISH. Endemic to Kauai.

Helodeaster helenae (Forbes & Lydgate) Nesom, **comb. nov.** *Lagenophora helenae* Forbes & Lydgate [as "helena"], Occas. Pap. Bishop Mus. Honolulu 6: 62. 1918. *Keysseria helenae* (Forbes & Lydgate) Cabrera, Blumea 14: 307. 1967. **TYPE: Hawaii**. **Kauai**. Swamp near Kaholuamano, "1915?," *J.M. Lydgate s.n.* (holotype: BISH image). Endemic to Kauai.

Helodeaster maviensis (H. Mann) Nesom, **comb. nov.** *Lagenophora maviensis* H. Mann, Proc. Amer. Acad. Arts 7: 172. 1867. *Keysseria maviensis* (H. Mann) Cabrera, Blumea 14: 307. 1967. **TYPE: Hawaii**. **Maui**. "Top of the mountain of West Maui," [1864-1865], *H. Mann & W.T. Brigham 440* (holotype: GH 9559 image; isotypes: GH 9560 image, K 890160 image). Endemic to Maui and Molokai.

A chromosome number of $2n = 54$ has been reported for *H. helenae* (Carr 1985) and *H. maviensis* (Mill 1990); chromosome numbers have not been reported for the Indonesian species.

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Figure 1. *Helodeaster maviensis*. Photo by J.K. Obata, Hawaiian Native Plant Genera, Univ. of Hawaii Botany Department.

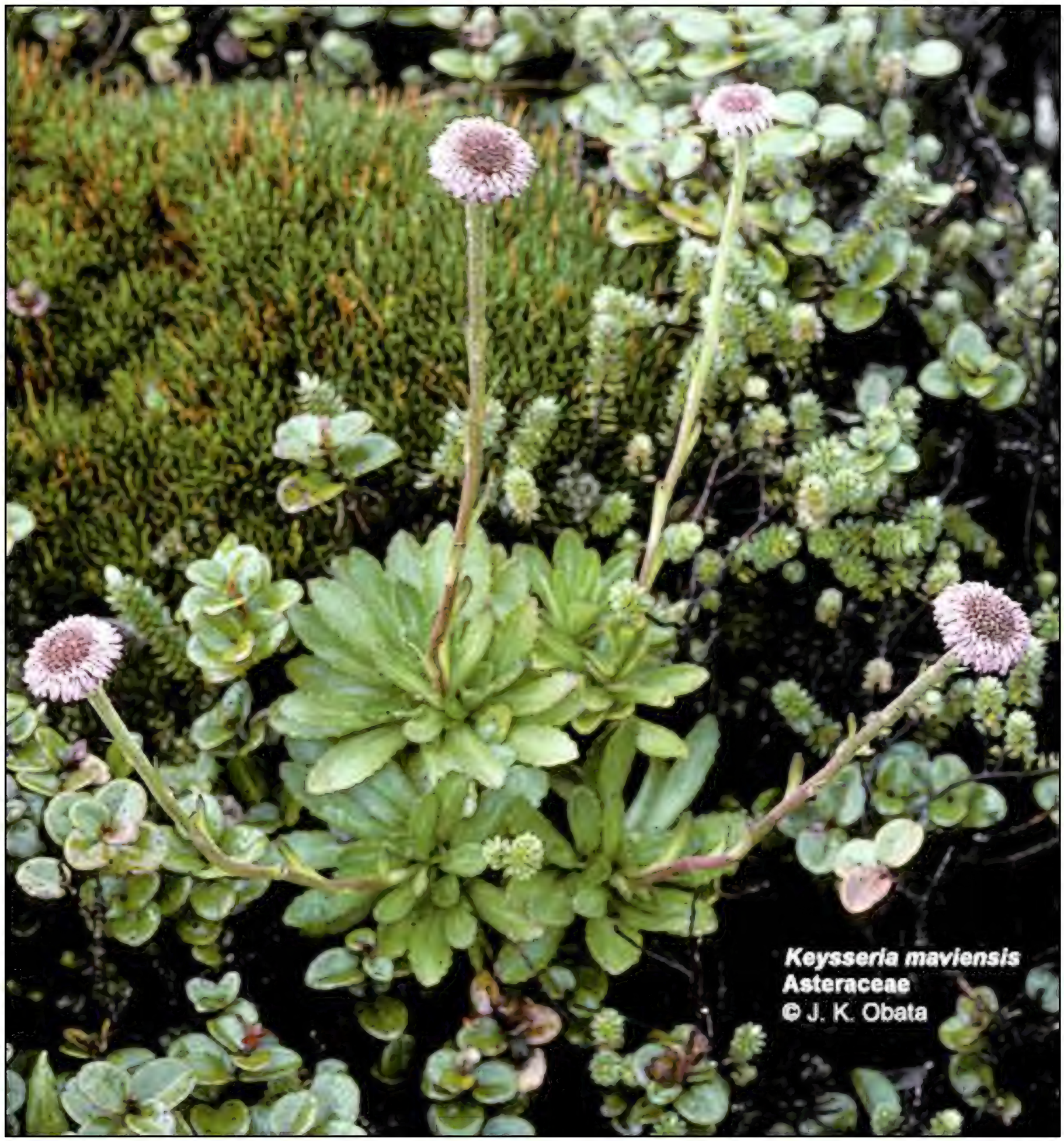

Figure 2. *Helodeaster maviensis*. Photo by J.K. Obata, Hawaiian Native Plant Genera, Univ. of Hawaii Botany Department.

Figure 3. *Helodeaster helenae*. USFWS photo, Wikipedia.

Figure 4. *Helodeaster helenae*. Photo by Oscar Johnson, iNaturalist.

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KITAMURIA, A NEW MONOTYPIC GENUS FOR *ASTER GLEHNII* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Aster glehnii (Japan, Sakhalin, and the Kuriles) is morphologically isolated among Asian species of *Aster*. Molecular data position it as most closely related to *Bellis* and *Tripolium* groups and similaries between *A. glehnii* and species of the *Tripolium* group support the insight from DNA clustering. *Aster glehnii* is recognized here as ***Kitamuria glehnii*** (F. Schmidt) Nesom, **comb. nov.**, constituting the monotypic **Kitamuria** Nesom, **gen. nov.**

Aster glehnii F. Schmidt, endemic to Japan, Sakhalin, and the Kuriles, is distinct from species of Asian *Aster* in the combination of morphological features noted below. Tamamshyan (1959) separated it as the monotypic ser. *Glehnianae* in his treatment of Russian *Aster*. Ito (1995) placed it within sect. *Aster*.

Molecular analyses (Ito et al. 1994; Ito et al. 1998; Lim et al. 2003; Shin et al. 2014) have indicated that *Aster glehnii* is distantly related to species of Japanese *Aster* (sensu lato, including *Heteropappus*, *Kalimeris* and *Miyamayomena*). The DNA analysis of Brouillet et al. (2009) placed *A. glehnii* in a position coordinate (trichotomous) with two other clades — *Tripolium*/*Galatella*/ *Crinitaria* and *Bellis*/*Bellium*/*Bellidiastrum*. The Brouillet et al. analysis calls to attention similarities between *A. glehnii* and the *Tripolium* group, especially in their rhizomatous habit, corymboid inflorescence, and densely glandular leaves and achenes. The *Bellis* group is distinct in morphology and a morphological connection to the others is obscure, but all three groups are tentatively associated as subtr. Bellidinae in Nesom (2020), emphasizing the molecular data. Evidence for the evolutionary isolation of *Aster glehnii* is recognized here by separating it as a distinct genus.

KITAMURIA Nesom, **gen. nov.** **TYPE**: *Kitamuria glehnii* (F. Schmidt) Nesom

Aster sect. *Amellus* ser. *Glehnianae* Tamamsch., Flora URSS 25: 92. 1959. **TYPE**: *Aster glehnii* F. Schmidt

Distinct among Asian species of *Aster* in the combination of its rhizomatous, herbaceous habit, tall stems, large, gland-dotted (abaxially) leaves, relatively few-flowered heads in a corymboid inflorescence, bright white rays, disc corolla lobes linear-lanceolate and cut nearly to the base of the limb, and elongate, compressed, gland-dotted achenes. Distinct from *Tripolium*/*Crinitina*/*Galatella* in its combination of large, petiolate, herbaceous leaves, ebracteate peduncles, bright white ray corollas, deeply cut disc corolla lobes, phyllaries of equal-length series, and pappus of basally distinct, persistent, non-accrescent bristles.

Kitamuria glehnii (F. Schmidt) Nesom, **comb. nov.** *Aster glehnii* [as glehni] F. Schmidt, Reis. Amur-Land., Bot., 146. 1868. **TYPE**: **RUSSIA**. **Sakhalin**. "Insula Sachalin," 10 Aug 1861, *Peter von Glehn s.n.* (holotype: LE; isotypes: GH image, K image, NY image-Figs. 1, 3).

Aster korsakoviensis H. Lév. & Van. in Repert. Spec. Nov. Regni Veg. 7: 103. 1909. **TYPE**: **RUSSIA**. **Sakhalin**. "Sagalien: In silvis," Korsakof, Sep 1908, *U.J. Faurie 752* (holotype: E image, Fig. 2).

Aster glehnii var. *hondoensis* Kitam, J. Jap. Bot. 11: 166. 1935. **TYPE**: **JAPAN**. [Nagano]. "Prov. Kaga, Dist. Hondo, Ichinose, in montibus," 27 Aug 1931, *S. Kitamura s.n.* (holotype: KYO, not seen).

Perennial herbs from a thick, creeping, woody rhizome. **Stems** erect, 70–150(–220) cm tall, with slightly zigzag nodes, softly hirsute. **Leaves** herbaceous, pinnate-veined (eucamptodromous to subbrochidodromous), basal withering at anthesis, cauline elliptic-lanceolate to lanceolate, 6–20 cm long, mostly 2.5–4 cm wide, petiole/petiolar region 2–15 mm long, apex long-acuminate-acute, base cuneate to cuneate-acute, margins shallowly serrate to serrulate-mucronulate with evenly spaced teeth, sometimes nearly entire, sparsely short-hirsute-strigose, gland-dotted abaxially. **Inflorescence** corymboid, heads on ebracteate (rarely bracteate) peduncles 4–20 mm long. **Involucres** 6–7 mm wide; receptacles alveolate, alveolar margins fimbriate; phyllaries narrowly lanceolate-oblong to narrowly lanceolate-elliptic, 4–5 mm long, in 2–3 series of equal to subequal length. **Ray flowers** fertile, 10–20, ligules bright white, 9–11 mm long, 1.5–2 mm wide, not coiling at maturity. **Disc flowers** fertile, ca. 6 mm long, becoming purplish with maturity, 5-lobed, lobes linear-lanceolate, cut 2/3 the length of the limb, recurving-coiling. **Achenes** narrowly oblanceolate-oblong, 3–3.5 mm long, strongly compressed, with 2 lateral nerves and sometimes a third on one of the faces, strigose-hirsute, gland-dotted; pappus of bristles in a single series, about equalling the disc corolla height, not accrescent, bristles apically acute. **Chromosome number**, 2n = 18.

Flowering August–October; grasslands and forest edges, rocky places in river valleys. Japan (Honshu, Hokkaido), Russia (Kuriles, Sakhalin). Plants identified as *Aster glehnii* from Korea instead are *Aster pseudoglehnii* Lim et al., which is closely related to *A. ageratoides* (Lim et al. 2003; Shin et al. 2014).

The genus name commemorates Siro Kitamura (1906-2002), specialist in Asteraceae and author of a comprehensive study of Japanese *Aster* (Kitamura 1937). He graduated from Kyoto University in 1931 and continued there with postgraduate studies. In 1932, with his academic supervisor Prof. Genichi Koidzumi and fellow students, he helped to establish the new journal *Acta Phytotaxonomica et Geobotanica*. Kitamura was appointed a research assistant at Kyoto in 1938 and Professor of Botany in 1945. He took part in collecting expeditions to Japan, Korea, northeast China, and Taiwan, as well as to Pakistan and Afghanistan, subsequently editing volumes of *Flora of Afghanistan* and *Plants of West Pakistan and Afghanistan*. He also produced five volumes of *Coloured Illustrations* of Japanese trees and herbaceous plants. After serving for 25 years as Director of the Kyoto Botanical Institute, Kitamura retired in 1970 (information mainly from Iwatsuki 2002; Anonymous 2013).

Aster glehnii var. *hondoensis* has been recognized from Honshu on the basis of slightly smaller leaves and heads and reduced vestiture (Ito 1995). Most collections identified as var. *hondoensis* documented on the GBIF website (https://www.gbif.org/occurrence/736054832) are from the montane region of central Honshu (Gunma, Nagano, Saitama, Yamanashi), where they apparently are sympatric with typical plants. Tamamshyan (1959) also noted the occurrence of variants (stem and peduncle thickness, leaf size, margins and apex) on Sakhalin and Shikotan islands. Whether these are populational or clinal variants is unknown.

Kitamuria glehnii has apparently convergent similarities to species of the eastern North American *Oclemena*. Plants of both genera are rhizomatous, herbaceous perennials and produce large, elliptic-lanceolate, abaxially gland-dotted leaves, few-rayed heads on ebracteate peduncles in corymbs, and elongate, gland-dotted achenes. *Oclemena* differs in its scale-like proximal cauline leaves, longer and nodding peduncles, erect, deltate disc corolla lobes, 4–8-nerved achenes with a 3-seriate inner pappus and short outer series.

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Figure 1. *Kitamuria glehnii*. Details from the NY isotype of *Aster glehnii*.

Nesom: *Kitamuria*, gen. nov.

Figure 2. *Kitamuria glehnii*. Details from the holotype of *Aster korsakoviensis* (E).

Figure 3. *Kitamuria glehnii*. NY isotype.

Figure 4. *Kitamuria glehnii*. Photo from <www7a.biglobe.ne.jp>, photographer unidentified.

Figure 5. *Kitamuria glehnii*. Photo by Takashi Hoshide, Flickr, identified as var. *hondoensis*.

Figure 6. *Kitamuria glehnii* from Sakhalin. Photo by Galina Chulanova from Plantarium <https://www.plantarium.ru/>.

Figure 7. *Kitamuria glehnii*. Photo by Sonny Ashimori, Flickr, identified as var. *hondoensis*.

Figure 8. *Kitamuria glehnii*. Above: Japan, photo by Koichi Oda, Wikispecies. Below: Sakhalin, photo by Tatyana Karmanova from Plantarium <https://www.plantarium.ru/>.

Figure 9. *Kitamuria glehnii*, cultivar "Agleni." Photo by Nora Goosen from Fotki.

Figure 10. *Kitamuria glehnii*, cultivar "Agleni." Photo from Gross Potrems Perennial Garden, Mecklenburg-West Pomerania <https://www.wildstaudenzauber.de/>

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THE GENUS *ASTER* (ASTERACEAE) IN THE STRICTEST SENSE

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ABSTRACT

Aster amellus L. (the type of *Aster* L.), *A. indamellus* Grierson, and *A. aitchisonii* Boiss. appear to comprise a natural group, as suggested by Grierson in 1964 — this is *Aster* in the strictest sense. A taxonomic summary is given for these species and a lectotype is designated for *Aster pseudamellus* Hook. f. Among species sampled for DNA sequence data, the closest relative of *A. amellus* is *A. alpinus*, which shares production of woody rhizomes with the *A. amellus* trio. *Aster maackii* also is indicated by molecular data to be closely related but produces non-woody rhizomes.

The genus *Aster* in Eurasia is morphologically diverse and evolutionarily complex. Recent molecular-phylogenetic analyses have shed light on the evolutionary relationships of these species although many species are yet to be included in the sampling. The most significant analysis (including the greatest number of species) for understanding patterns has been that of Li et al. (2012) — subsequent studies have signficantly added to the Li et al. data set (e.g., Jafari et al. 2015; Korolyuk et al. 2015; Zhang et al. 2015; Fu et al. 2019). A distinct pattern emerges and has been discussed in detail by Li et al.

In parallel with restructuring the subtribal taxonomy of Astereae (Nesom 2020a), I have initiated a revision of *Aster* taxonomy, recognizing new genera indicated by molecular data to be distinct, providing morphological characterizations, and using morphology to find related species not included in the molecular sampling. As with the subtribal taxonomy, and as always, these newly recognized genera are hypotheses to be tested by further sampling of species and analysis of morphological and molecular data.

Studies of Astereae and *Aster* have been done over the spring and summer of 2020, using pertinent literature and online images available through JSTOR and various herbaria and consortia that post specimen images and related information. Details of trichomes and florets are difficult to observe but packet dissections sometimes are included in images and, overall, a surprisingly large amount of information is available.

Eurasian asters primarily occur in three main clades, with a few 'grade' species — most have been placed in subtribe Asterinae (Fig.1, duplicated here from Nesom 2020a). Li et al. (2012) considered *Aster* sensu stricto to comprise species of the **Asterothamnus branch** and **Aster branch** and recognized that species of the **Psychrogeton branch** and **Hersileoides branch** should be placed in genera outside of strictly defined *Aster*. The **Asterothamnus branch** is excluded here from *Aster* as it includes clearly defined and generally accepted genera (i.e., *Asterothamnus* and *Arctogeron*; *Kemulariella* has not been included in molecular sampling but appears to belong in this clade; the position of *Rhinactinidia* is ambiguous but morphology and geography favor its placement here [Nesom 2020a]; *Cardiagyris*, *Chaochienchangia*, and *Sinobouffordia* are morphologically and molecularly distinct). Newly proposed genera, including a total of 64 species) in the branches of Figure 1 are validated and detailed in publications contemporary with this one.

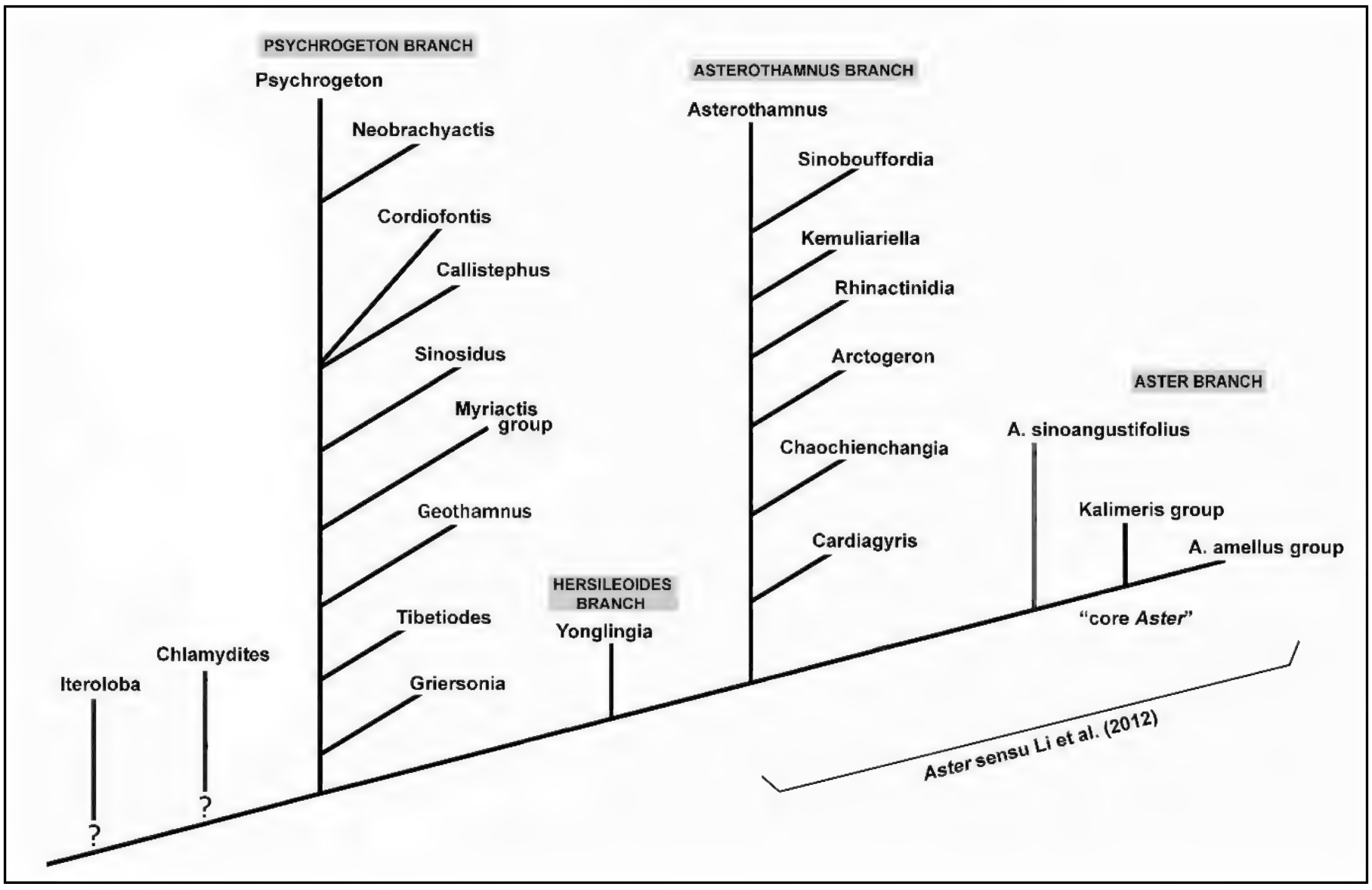

Figure 1. Astereae subtribe Asterinae (from Nesom 2020a). An intuitively constructed consensus tree, summarizing published phylogenetic analyses based on DNA sequence data. The diagram position of some taxa is speculative, chosen from among ambiguous placements in molecular phylogenies or placed by morphology if not included in molecular sampling.

Even in its restricted definition, *Aster* (**core Aster**, sensu Fig. 1) remains morphogically heterogeneous. The phylogenetic structure of **core Aster** may become more complex as more species are sampled, and some of the species groups may ultimately be accepted at generic rank.

The **Kalimeris group** includes *Kalimeris*, *Heteropappus*, *Miyamayomena*, *Sheareria*, and the 'ageratoides' group (*Aster* sect. *Ageratoides* sensu stricto plus other species in the larger *A. ageratoides* clade (Nesom 2020a for details). The **Aster amellus group** includes *A. amellus* (the type of the genus), *A. alpinus*, *Rhynchospermum*, *Turczaninovia*, and a group of other distinctive species in largely unresolved phylogenetic placement.

The Li et al. analysis places *Aster alpinus* (Figs. 15–18) as sister to *A. amellus* but additional species probably will modify this interpretation (especially *A. indamellus* and *A. aitchisonii* and species potentially closely related to *A. alpinus*). Onno's ser. *Macrochaeti* subser. *Alpini* (1932, p. 7) included *A. alpinus* and 11 other monocephalous species of otherwise highly disparate morphology. In *Aster* sect. *Alpinaster* (type, *A. alpinus*), Tamamshyan (1959) included morphologically complex *A. alpinus* and four other species: *A. fallax*, *A. korshinskyi*, *A. serpentimontanus*, and *A. tolmatschevii*. In *Aster* ser. *Alpini* (type, *A. alpinus*), Ling (1985) included *A. alpinus* (including varieties) and nine other species (of these nine, *A. handelii*, *A. heterolepis*, and *A. oreophilus* cluster with the *A. ageratoides* clade of the **Kalimeris group** (Li et al. 2012); the other six are molecularly unsampled). *Aster* sect. *Alpigeni* of Chen et al. (2011) includes 44 species — including *A. alpinus* with four varieties and *A. oreophilus* and *A. heterolepis*, which, based on their key to species, appear to be most closely similar to *A. alpinus*.

Aster amellus and *Aster* in its strictest sense

In discussion of *Aster indamellus* (a replacement name for *A. pseudamellus* Hook. f.), Grierson (1964, p. 88) provided a hypothesis that serves as a starting point for a strict definition of *Aster*. *Aster indamellus* "is one of a group of related species the common ancestor of which must once have been widespread in the continent of Asia. It appears to have given rise to *A. amellus* in Europe, *A. indamellus* and *A. aitchisonii* in the Western Himalaya, *A. maackii* in Eastern Siberia, and although less closely allied, probably also to *A. vestitus* and *A. poliothamnus* in the East Himalaya regin. Of these *A. indamellus* is most closely related to *A. amellus*."

Plants of *Aster amellus*, *A. indamellus*, and *A. aitchisonii* (Figs. 2–11) are subshrubs — they have persistent, woody stem bases and woody or lignescent caudex branches or rhizomes (rhizomes becoming caudex branch-like?). Phyllaries are strongly graduate in length. *Aster indamellus* and *A. aitchisonii* have not been included in molecular analyses, but the hypothesis here predicts that this is a monophyletic group, *Aster* in the strictest sense. *Aster alpinus* is similar in habit (woody caudex/rhizomes) but is monocephalous and phyllaries are equal to subequal in length. The similarity between *A. amellus* and *A. alpinus* in proximal woodiness appears to be a specialized feature indicating common ancestry — all other species in the **Aster amellus group** also are rhizomatous but the rhizomes are non-woody (personal observation; Chen et al. 2011).

Molecular data place *Aster maackii* (Figs. 12–14) in the **Aster amellus group** (Fig. 1) but the species does not appear to be in the immediate relationship of *A. amellus* and *A. alpinus*. The analysis of Zhang et al. (2015) places *A. maackii* as sister to *A. piccolii*, which is remarkably similar in morphology, except for the reduced pappus of the latter. *Aster maackii* and *A. piccolii* resemble *A. indamellus* and *A. aitchisonii* in inflorescence form, strictly erect stems, toothed leaves, and strongly graduate phyllaries, but the plants are herbaceous perennials arising from short, densely fibrous-rooted, non-woody rhizomes. *Aster vestitus* is in the **Kalimeris group** and relatively distantly related to *A. amellus*. *Aster poliothamnus* (in the **Asterothamnus branch**) is even more distantly related and has been included in the genus *Sinobouffordia* (Nesom 2020b).

Taxonomic summary of typical *Aster* L.

1. **Aster amellus** L., Sp. Pl. 2: 873. 1753. **LECTOTYPE** (Semple 2006): **Europe**. Habitat in Europae australis asperis collibus, Herb. Linn. 997.16 (LINN). Figures 2 and 3.

Montane habitats from central France and northern Italy eastward to Belarus, Ukraine, and southeastern Russia, and into Turkey, Georgia, Armenia, Azerbaijan, and Iran (see map in Münzbergová et al. 2011).

Aster amellus is a polymorphic aggregate including diploids, tetraploids, and hexaploids (summary in Münzbergová et al. 2011). Three species within the aggregate were recognized by Tamamshyan in his *Aster* ser. *Amelliae* (1959, 89–92): *A. amellus*, *A. ibericus* Stev., and *A. amelloides* Bess., supported by morphology, chromosome number, and geography. Tzvelev (2002) treated *A. amellus* with three subspecies, corresponding to the species above: subsp. *amellus*, subsp. *ibericus* (Stev.) Avetisjan, and subsp. *bessarabicus* (Rchb.) Soó. More recent cytological studies, however, as well as isozyme and cpDNA analyses, support the treatment of *A. amellus* as a single polymorphic species instead of multiple independent taxa (summary in Münzbergová et al. 2011). Ling's *Aster* ser. *Amelli* (1985, 134–135) is typified by *A. amellus* but it includes only *A. indamellus* (*A. amellus* and *A. aitchisonii* do not occur in China).

2. **Aster indamellus** Grierson [nom. nov.], Notes Roy. Bot. Gard. Edinb. 26: 87. 1964. *Aster pseudamellus* Hook. f., Fl. Brit. India 3: 249. 1881 (not Wenderoth 1831). **LECTOTYPE** (designated here): **INDIA**: **Uttarakhand**. Kumaon, Pangi, Kanawar, 8-9000 ft, 18 Aug 1847, *T. Thomson s.n.* (K 890408 image). Figures 7 and 8. Protologue: "Western Himalaya,

Jacquemont; Kumaon, alt. 8-9000 ft, *Thomson*. Lahul, *Jaeschke*." The collections by Jacquemot and Jaeschke also are at K.

Afghanistan, China (Xizang: Mt. Xixabangma, Yang Si), India (Himachal Pradesh, Punjanb, Uttarakhand), Kashmir, Nepal, Pakistan.

Grierson (1964, p. 89) noted that *Aster amellus* and *A. indamellus* "generally resemble one another in habit, but *A. amellus* is less leafy and usually eglandular. Furthermore, its phyllaries are mostly obtuse, imbriate and distinctly ciliate." Leaf margins of *A. indamellus* and *A. aitchisonii* usually are serrate with 1–3(–4) pairs of teeth, while those of *A. amellus* are consistently entire or shallowly and nearly indistinctly toothed.

3. Aster aitchisonii Boiss., Fl. Orient. [Boissier] Suppl. 287. 1888. **TYPE**: **PAKISTAN**. Kurrum Valley plants, Shid Doi, shrub on rocks, 7000-8000 ft, 11 Jul 1879, *J.E.T. Aitchison 812* (holotype: G fide Grierson 1964, photo & fragment-E; isotypes: BM image, K image-Figs. 9 and 11, S image). Protologue: "Hab. ex rupibus verticalibus pendulus in valle Kuran Affghaniae 7-8000 ft (Aitch. 812)."

Paratype: **Afghanistan [Pakistan]**. Chapri, Shid Doi Naba, hanging from rocks, 7000 m, 14 Jul 1880, *Aitchison 323* (BM as cited by Grierson, K image-Fig. 10).

Apparently known only from the type locality or immediate area. Dr. (Surgeon Major) Aitchison made the type collection and his "323" near the end of the Second Anglo-Afghan War — the label locality is noted as Afghanistan but the Kurram Valley is in western Pakistan.

Aster aitchisonii is distinguished from *A. amellus* and *A. indamellus* "by the smaller size of its capitula and also by its tougher xerophytic habit. The stems tend to be densely leafy and on the peduncles the uppermost leaves overlap and to some extent become confused with the lowermost phyllaries. In *A. aitchisonii*, however, the leaves are always pale greyish-green and bear a few sharp-pointed teeth on the margins, the phyllaries are coriaceous, completely lacking the foliaceous tips of *A. indamellus*, and their margins are fringed with fine white cilia" (Grierson 1964, p. 89).

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Figure 2. *Aster amellus*. Lectotype, Herb. Linn. 997.16 (LINN).

Figure 3. *Aster amellus*. Details from the lectotype, Herb. Linn. 997.16 (LINN).

Figure 4. *Aster amellus*. Turkey, *Winter 218* (US). Woody rhizomes, lignescent stem bases.

Figure 5. *Aster amellus*. Turkey, *Balls 1983* (E). Woody rhizomes, lignescent stem bases.

Figure 6. *Aster amellus*. Turkey, *Davis 46665* (E). Woody rhizomes, lignescent stem bases.

Figure 7. *Aster indamellus*. Lectotype, *Thomson s.n.* (K).

Figure 8. *Aster indamellus*. Details from lectotype, *Thomson s.n.* (K).

Figure 9. *Aster aitchisonii*. Isotype, *Aitchison 812* (K).

Figure 10. *Aster aitchisonii*. Paratype, *Aitchison 323* (K).

Figure 11. *Aster aitchisonii*. Details from K isotype.

Figure 12. *Aster maackii*. Russia. *Solomon & Barkalov 19608* (US).

Figure 13. *Aster maackii*. Russia. *Якуов s.n.* (US).

Figure 14. *Aster maackii*. Russia. *Solomon & Barkalov 19883* (US).

Figure 15. *Aster alpinus*. Germany. *Schuhwerk 92/248* (US).

Figure 16. *Aster alpinus*. Russia. *Elias et al. 803B* (US).

Figure 17. *Aster alpinus*. China. (HMC).

Figure 18. *Aster alpinus*. Russia. *Joukov s.n.* (KUN).

Nesom, G.L. 2020. *Yonglingia*, *Chaochienchangia*, and *Sinobouffordia* (Asteraceae: Astereae), new genera segregated from *Aster* in China. Phytoneuron 2020-57: 1–25. Published 19 August 2020. ISSN 2153 733X

YONGLINGIA, *CHAOCHIENCHANGIA*, AND *SINOBOUFFORDIA* (ASTERACEAE: ASTEREAE), NEW GENERA SEGREGATED FROM *ASTER* IN CHINA

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ABSTRACT

Two species of *Aster* are placed here in **Yonglingia** Nesom, **gen. nov.**, as ***Yonglingia hersileoides*** (Schneid.) Nesom, **comb. nov.**, and ***Yonglingia nitida*** (C.C. Chang) Nesom, **comb. nov.** **Chaochienchangia** Nesom, **gen. nov.**, includes ***Chaochienchangia falcifolia*** (Hand.-Mazz.) Nesom, **comb. nov.** **Sinobouffordia** Nesom, **gen. nov.**, includes ***Sinobouffordia poliothamnus*** (Diels) Nesom, **comb. nov.**, and ***Sinobouffordia sikuensis*** (Smith & Farrer) Nesom, **comb. nov.** Plants of *Yonglingia* and *Sinobouffordia* are shrubs; those of *Chaochienchangia* are herbaceous perennials; each of the three genera is endemic to China and characterized by solitary heads on axillary branches. In molecular analyses *Chaochienchangia* and *Sinobouffordia* are part of the *Asterothamnus* branch of subtribe Asterinae, while *Yonglingia* is sister to the combined *Asterothamnus*/"core *Aster*" branches.

As part of a taxonomic revision of tribe Astereae (Nesom 2020a), monophyletic species and species groups of Asian *Aster* unequivocally indicated by molecular data to be outside of "core Aster" (sensu Li et al. 2011) are given generic rank. This manuscript recognizes three new genera from the "Asterothamnus branch" — a fourth genus, *Cardiagyris* (Fig. 1), is described in a separate paper (Nesom 2020b).

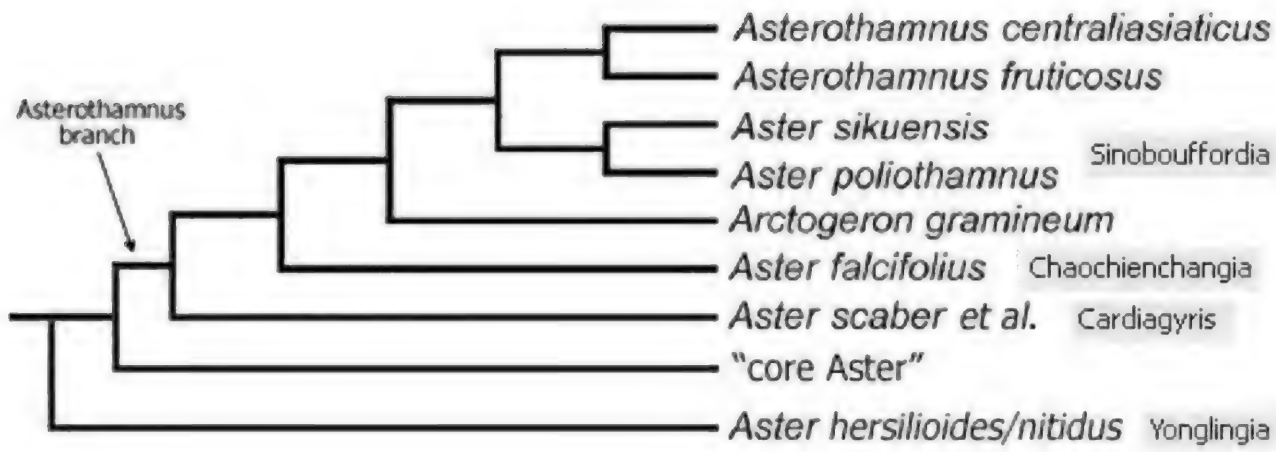

Figure 1. Evolutionary relationship of *Yonglingia*, *Chaochienchangia*, and *Sinobouffordia*, based on combined ITS, ETS and trnL-F data. Modified from Zhang et al. (2015). Part of subtribe Asterinae (Nesom 2020a).

YONGLINGIA Nesom, **gen. nov.** **TYPE**: *Yonglingia hersileoides* (C.K. Schneid.) Nesom
Aster ser. *Hersileoides* Y. Ling, Fl. Reipubl. Pop. Sin. 74: 177, 357. 1985. Type: *Aster hersileoides* C.K. Schneid.

Distinct in its perennial, shrubby-sprawling habit, eglandular vestiture, solitary heads terminal and diffusely arranged on axillary, few-bracteate branches, 2–4 nerved, eglandular achenes, and 2-seriate pappus of apically clavate bristles.

Shrubs. **Stems** 50–150 cm tall, erect to ascending or sprawling; leaf scars and axillary buds prominent; young branches purplish to reddish, usually hairy in decurrent lines below leaves; older stems apparently with secondary growth and up to 4 mm wide. **Leaves** cauline, narrowly obovate-oblanceolate to

elliptic-lanceolate, surfaces glabrous except for abaxial midvein, eglandular, margins entire to shallowly serrate. **Heads** solitary, terminal on second-year axillary branches; involucres campanulate, 2.5–3 cm wide (pressed); phyllaries in 3–4 graduate series, glabrous, oblong-lanceolate with acute apices, with a dark, slightly translucent, oblong to fusiform-lanceolate medial region, sometimes basally indurate proximally; receptacles alveolate. **Ray flowers** 18–30, ligules 9–13 mm long, 1–2.5 mm wide, coiling, white to pink or light purple. **Disk flowers** fertile, corollas cylindric, 3.5–4 mm long, limb gradually broadening above the tube, sparsely hairy, eglandular, lobes triangular, spreading to recurving. **Achenes** elliptic-oblong, 2–3 mm long, compressed with 2 lateral veins plus 1 on each face, sparsely short-strigose, eglandular; pappus 2-seriate, inner of subequal bristles 3.5–4 mm long, apically acute or sometimes innermost clavate, outer of slender bristles 0.5–1 mm long. Base chromosome number, x = 9.

The genus commemorates Yong Ling (1903-1981), expert on Asteraceae at the Institute of Botany (PE), Chinese Academy of Sciences. He became Chief Editor of the Flora Reipublicae Popularis Sinicae in 1973 (Ma & Clemants 2006) and was co-editor of the Asteraceae (Vol. 74) and author of the *Aster* treatment (Ling 1985).

The morphological distinction of the Chinese species *Aster hersileoides* and *A. nitidus* has been previously recognized — they were placed together as *Aster* ser. *Hersileoides* (Ling 1985). Recent molecular-phylogenetic analyses indicate that they are evolutionarily isolated, comprising a group outside of what W.-P. Li et al. (2012) considered as *Aster* sensu stricto (the same phylogenetic topology shown by Zhang et al. 2015 and Z. Li et al. 2017, and essentially the same summarized by Nesom 2020a). Li et al. (2012) noted that it might be reasonable to treat these two species as a separate genus.

1. Leaves elliptic-oblanceolate to narrowly obovate, 1–3 cm long, apex acute to obtuse, margins short-ciliate with stiffly spreading hairs ..... **Yonglingia hersileoides**

1. Leaves lanceolate, 2.5–6.5 cm long, apex acuminate, margins without spreading cilia ..... **Yonglingia nitida**

1. Yonglingia hersileoides (C.K. Schneid.) Nesom, **comb. nov.** *Aster hersileoides* C.K. Schneid. in Sargent, Pl. Wilson. 3: 459. 1917. **TYPE**: **CHINA**. **Sichuan**. "Maochon, western Szechuan" [= Mao Xian], 5000 ft, 24 May 1908, *E.H. Wilson 2234* (holotype: A-Fig. 2; isotypes: A-Fig. 4, E-Fig. 3).

Leaves narrowly elliptic-oblanceolate to narrowly obovate, epetiolate, 1–3 cm long, 3–7 mm wide, herbaceous, surfaces glabrous or adaxial midvein hairs, apex acute to obtuse, rounded, or truncate, apiculate to mucronulate, margins entire or rarely with 1 pair of sharp teeth, stiffly spreading-ciliate with short hairs, venation camptodromous to nearly brochidodromous. Chromosome number (Yin et al. 2010), $2n = 18$.

Flowering April-July. "Dry slopes on hills, rocky walls; 1300–2800 m" (FOC). Sichuan.

2. Yonglingia nitida (C.C. Chang) Nesom, **comb. nov.** *Aster nitidus* C.C. Chang, Bull. Fan Mem. Inst. Biol., Bot. 6: 47. 1935. **LECTOTYPE** (Qi & Zhi-Rong 2010): **CHINA**. **Chongqing**. Nanchuan, 1100 m, 29 Apr 1932, *T.H. Tu 2935* (PE 00029973, Fig. 5). Two collections were cited in the protologue.

Syntype: **CHINA**. **Sichuan**. Pangou [= Pujiang Xian, Pangou], under woods, 820 m, April 1932, *T.H. Tu 2849* (PE, Fig. 6).

Leaves lanceolate, epetiolate or with a short subpetiolar region, 2.5–6.5 cm long, 5–18 mm wide, smaller on youngest branches, subcoriaceous, shiny adaxially, surfaces glabrous or adaxial veins hispidulous proximally, apex gradually narrowed to a sharply acute apex, margins entire or serrate with 1–4 pairs of teeth, glabrous to sparsely strigose, venation supra-basal acrodromous. Chromosome number (Yin et al. 2010), $2n = 18$.

Flowering February-May. "Forests on hills, streamside rocks; 500–1100 m" (FOC). Sichuan, Chongqing, Hubei, Yunnan.

Figure 2. *Yonglingia hersileoides*. Sichuan. Holotype (A).

Figure 3. *Yonglingia hersileoides*. Stem from isotype (E).

Figure 4. *Yonglingia hersileoides*. Head from isotype (A).

Figure 5. *Yonglingia nitida*. Chongqing. Lectotype (PE).

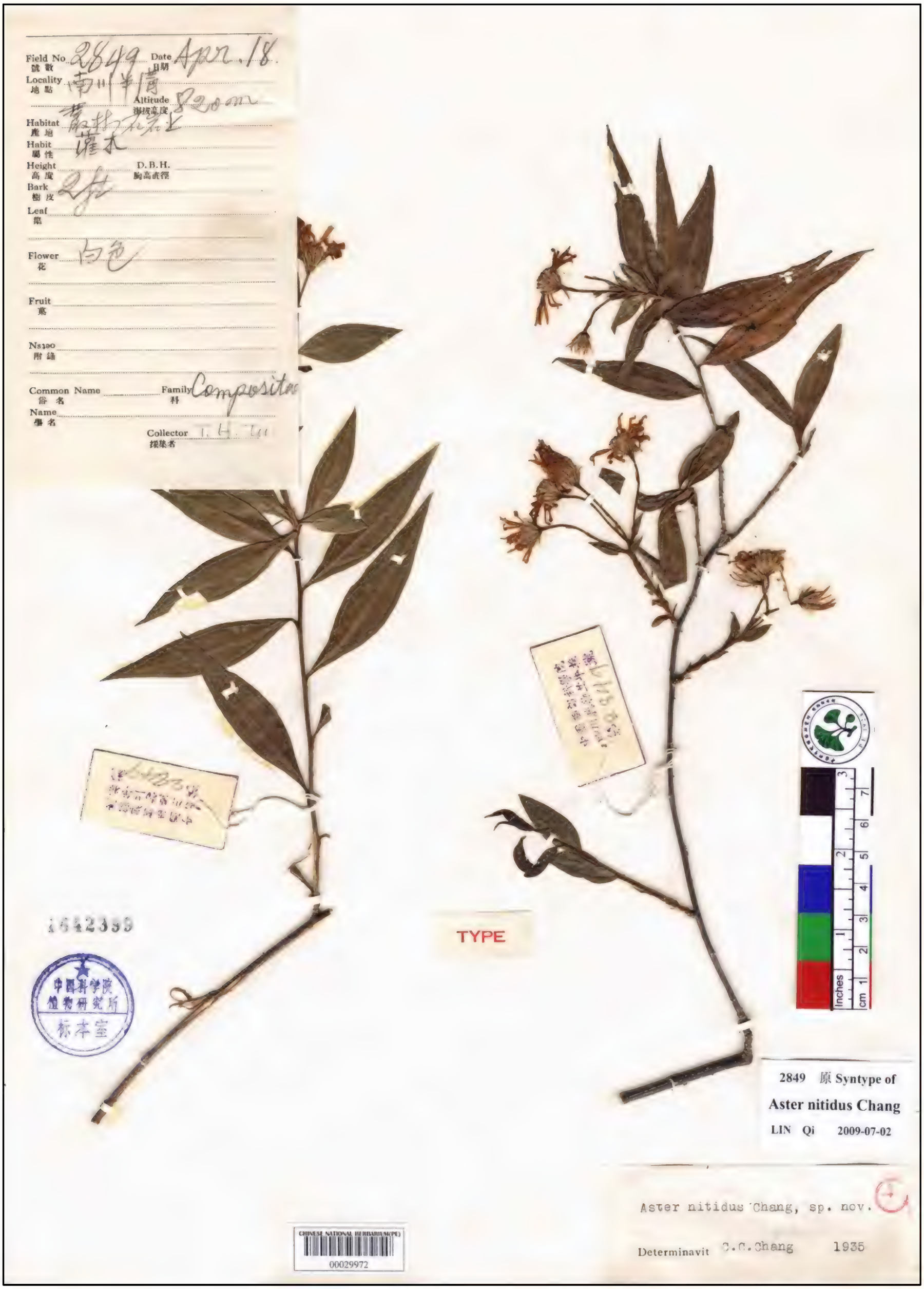

Figure 6. *Yonglingia nitida*. Sichuan. Syntype (PE).

Figure 7. *Yonglingia nitida*, bright-leaf aster. Flora of Sichuan and Chongqing website. The inflorescence and leaf margins match those of the lectotype. The shiny leaf surfaces are alluded to by the epithet.

CHAOCHIENCHANGIA Nesom, **gen. nov.** **TYPE**: *Changia falcifolia* (Hand.-Mazz.) Nesom

Distinct in its herbaceous-perennial, rhizomatous habit, ovate-acuminate leaves, glandular stems, leaves, phyllaries, and achenes, solitary heads terminal on short, axillary, bracteate branches, linear, herbaceous, loose and sometimes squarrose phyllaries, 2-ribbed achenes, and multiseriate pappus of apically clavate bristles.

Perennial herbs, from an abbreviated caudex and slender, woody rhizomes. **Stems** 30–60 cm tall, erect, loosely strigose, minutely stipitate-glandular, often resinous. **Leaves** cauline, lowest withered by anthesis, mostly lanceolate to ovate-acuminate, 1–9 cm long, short-petiolate (petioles 1–3 mm long), base rounded to obtuse, apex acuminate to falcate-acuminate, margins entire or distally serrate with 1–3 pairs of sharp teeth, glabrous and punctate-glandular abaxially, adaxially scabrous and minutely stipitate-glandular on veins, slightly resinous; venation eucamptodromous, often with a strong suprabasal pair. **Heads** solitary, terminal on short, bracteate, axillary branches 1–20(–60) mm long, sometimes distributed along much of stem, bracts grading into phyllaries. **Involucres** campanulate, 10–14 mm wide (pressed); phyllaries in 3–4 subequal series, mostly linear-oblong to linear-lanceolate, herbaceous, apically acute, loose and often squarrose, with distinct midvein and 3–7 dark green striae, strigose, minutely stipitate-glandular and often resinous, often purplish apically. **Ray flowers** 30–35, ligules 8–10 mm long, white to lavender, tardily coiling. **Disk flowers** bisexual, fertile, corollas 6–7 mm long, eglandular, lobes triangular, spreading. **Achenes** oblong, 2.7–3 mm long, compressed, 2-ribbed, strigose, sparsely stipitate-glandular; pappus of barbellate bristles in 4 series of unequal length, the inner about as long as the disc corollas, weakly clavate apically, outermost 0.4–0.8 mm long.

The genus name commemorates Chao-Chien Chang (1900-1972; Zhao-Qian Zhang; C.C. Chang), a long-time student of Chinese *Aster* and Asteraceae as well as other families. He graduated from the Department of Biology of National Southeast University (Nanjing in Jiangu Province) in 1926 and by 1928 was Assistant Curator in the herbarium there. His correspondence in May and June 1928 with the Director at Kew regarding an exchange of 200 specimens from Jiangsu is on record at K (via JSTOR Global Plants).

C.C. Chang was a researcher and acting director of the South China Institute of Botany (Guangzhou), Chinese Academy of Sciences, where he expanded it to include plant taxonomy, plant ecology, geobotany, plant physiology, and plant biology. He became part of the Fan Memorial Institute of Biology, which moved to Beijing with the end of WWII, and was appointed in 1955 to the faculty of the Chinese Academy of Sciences. The main set of his personal collections is at IBSC (South China Botanical Garden, Guangzhou).

Chaochienchangia falcifolia (Hand.-Mazz) Nesom, **comb. nov.** *Aster falcifolius* Hand.-Mazz., Notizbl. Bot. Gart. Berlin-Dahlem. 13: 610. 1937. **TYPE MATERIAL**: **CHINA**. **Hubei**. "W. Hupeh," July 1900, *Wilson with Veitch Exped. 1563* (K image, Fig. 8). Protologue: "W-Hupeh (Henry 1034); VII. 1900 (Wilson, Veitch Exp. 1563, Typus: Hb. Berlin, Mus. Wien)."

Aster brachyphyllus C.C. Chang, Bull. Fan Mem. Inst. Biol. Bot. 6: 44. 1935 (not *Aster brachyphyllus* (Sonder) F. Muell. 1865). **TYPE**: **CHINA**. **Sichuan**. Baoxing xian, Len-mo-gou, roadside, 950 m, Oct 1933, *H. Tu 4788* (holotype: PE image!, cited in protologue as "Sci. Soc. Nanking Biol. Lab. Herb.").

Slopes, roadsides, stream banks, rock outcrops; 600–1800 m. Gansu, Hubei, Shaanxi, Sichuan.

The protologue of *Aster falcifolius* compared it to *A. turbinatus* S. Moore, which also produces solitary heads on short axillary branches, but *A. turbinatus* is highly distinctive, differing from *A. falcifolius* in leaf, involucral, and achene morphology and vestiture. Molecular data (Li et al. 2012) indicate that the evolutionary position of *A. turbinatus* is among species of the *Aster amellus* group, where its involucral morphology is similar to *A. baccharoides* and *A. jishouensis*.

Figure 8. *Chaochienchangia falcifolia*. Type material of *Aster falcifolius*, "W. Hupeh, July 1900," *Wilson 1563* (K). Annotated by C.C. Chang as *Aster nitidus*.

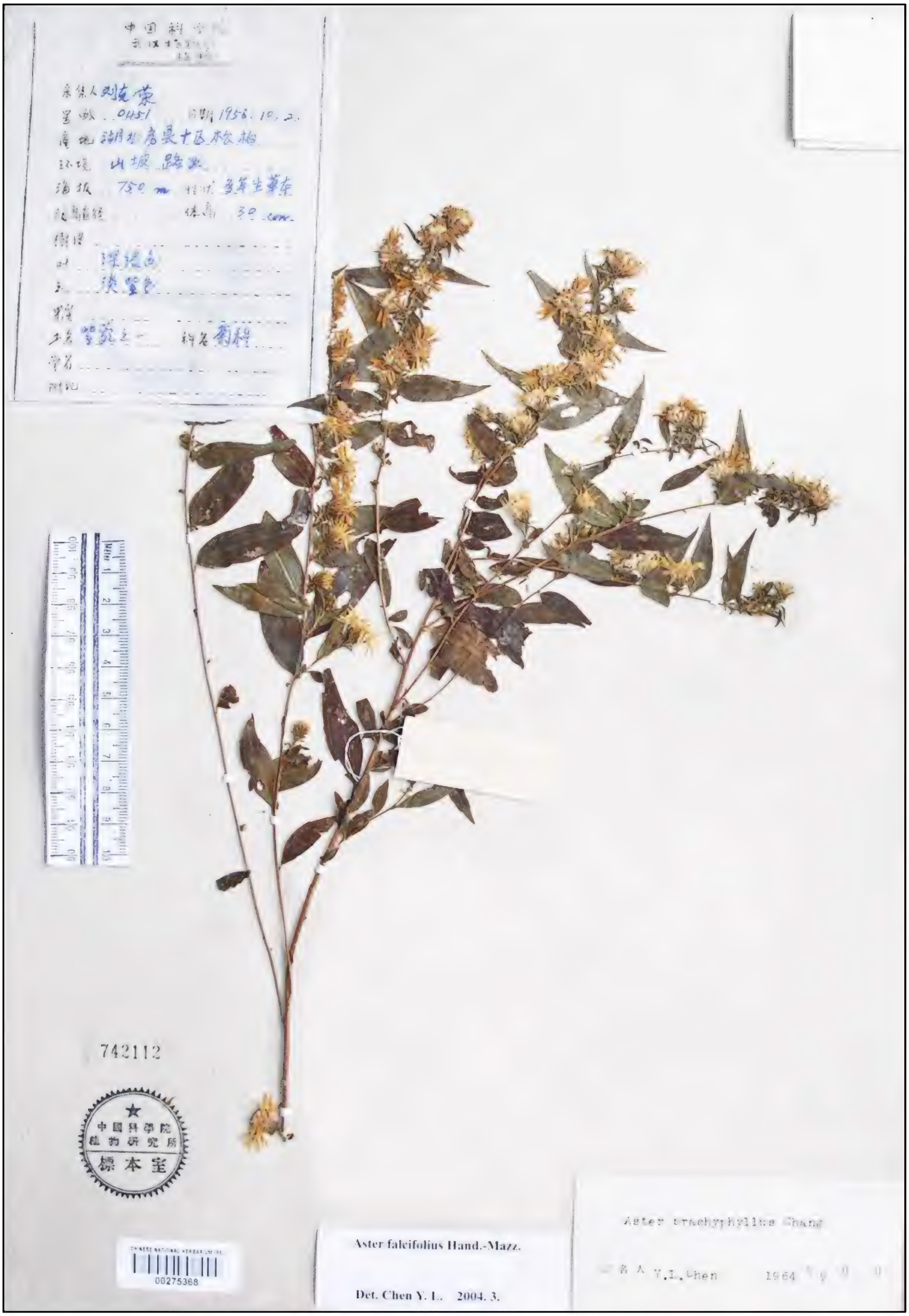

Figure 9. *Chaochienchangia falcifolia*. Hubei, *Kerong 451* (PE).

Figure 10. *Chaochienchangia falcifolia*. Sichuan, *236 Sichuan Task Force 977* (PE).

Figure 11. *Chaochienchangia falcifolia*. Sichuan, *Yeqi 2046* (PE).

Figure 12. *Chaochienchangia falcifolia*. Hubei, *1980 Sino-American Botanical Exped. 1619* (E).

SINOBOUFFORDIA Nesom, **gen. nov.** **TYPE**: *Sinobouffordia poliothamnus* (Diels) Nesom

Shrubs from a woody taproot and short, woody, branching caudex, leaves densely arranged, epetiolate, glandular on both surfaces, heads small and solitary at ends of unbranched, leafy-bracteate branches, phyllaries strongly graduate, and achenes compressed, ellipsoid. Similar to *Yonglingia* in its shrubby habit, densely leafy stems, and solitary heads terminal on axillary branches but distinct in its glandular vestiture, more numerous and much smaller heads on leafier peduncles, phyllaries more indurate-scarious, and pappus bristles with tapering, flattened tips.

Shrubs from a woody taproot and woody caudex branches. **Stems** 15–100 cm tall, densely leafy, minutely stipitate glandular, hirsutulous or puberulent. **Leaves** narrowly oblong to narrowly oblong-lanceolate or oblong-elliptic, base attenuate to obtuse or rounded, epetiolate, not decurrent, apex acute to obtuse, margins entire, midcauline mostly 7–21 mm long, both surfaces dark green and gland-dotted. **Heads** solitary at ends of leafy-bracteate branches 1.5–10 cm long, numerous in a subcorymboid array. **Involucres** campanulate, 6.5–9 mm wide (pressed); phyllaries 4–5-seriate, strongly graduate in length, lanceolate with acute or rounded-obtuse apex, indurate, narrowly keeled, inner stramineous, outer and middle stramineous with a herbaceous, stipitate-glandular apical portion; receptacles epaleate. **Ray flowers** 12–22, ligules 6–10 mm long, coiling, white to lavender or light purple. **Disc flowers** bisexual, fertile, corollas 3.5–5 mm long, tube abruptly widening into the limb, lobes deltate-triangular, spreading to recurving. **Achenes** ellipsoid, 2–2.5 mm long, compressed, 2–3-ribbed, sparsely strigose, minutely stipitate glandular; pappus of barbellate bristles 2.5–5 mm long with tapering, flattened tips, outermost much shorter, 0.1–0.5 mm long.

The genus name commemorates Dr. David Boufford, Senior Research Scientist, Harvard University Herbaria, who has had a long-standing interest in the flora of China and southeast Asia (e.g., Boufford & Spongberg 1983; Ying, Boufford, & Zhang 1993). He has organized and participated in collecting trips in southwest China for three decades, contributed his collections, field notes, and photographs toward databases (e.g., Biodiversity of the Hengduan Mountains Project 2020), and served as a major editor for the new English language Flora of Japan, the Flora of China, Flora of Taiwan (ed. 2), the Flora of Korea, and the Flora of North America North of Mexico. With Ray Angelo of the New England Botanical Club, he published an annotated atlas of the New England flora. The name has long been in mind but the more direct version was preempted by *Bouffordia* H. Ohashi & K. Ohashi (K. Ohashi et al. 2018), a genus of Fabaceae, also named for Dave.

Plants of *Sinobouffordia* are shrubs from woody taproots, an unusual habit among asters but one that is matched in *Asterothamnus*. They are remarkably similar to *Yonglingia* (this manuscript, especially *Y. hersileoides*) in their shrubby habit, densely leafy stems, and solitary heads on axillary branches but *Yonglingia* is more distantly related (Fig. 1).

Aster poliothamnus and *Aster sikuensis* are indicated to have a sister relationship in the analysis of Li et al. (2011). The analysis of Zhang et al. (2015) shows the pair as sister to *Asterothamnus* (Fig. 1). These species are part of the *Asterothamnus* branch of subtribe Asterinae (Nesom 2020a) and treated here apart from a more narrowly defined *Aster* L.

1. Leaf and phyllary surfaces evenly hirsutulous; phyllaries lanceolate-triangular, apices acute ..... **Sinobouffordia poliothamnus**
1. Leaf and phyllary surfaces puberulent-hirsute with soft hairs; phyllaries elliptic-lanceolate, apices rounded-obtuse ..... **Sinobouffordia sikuensis**

1. Sinobouffordia poliothamnus (Diels) Nesom, **comb. nov.** *Aster poliothamnus* Diels in Limpricht, Repert. Spec. Nov. Regni Veg. Beih. 12: 503. 1922. **TYPE**: **CHINA**. **Sichuan**. "Dege—Bejü, Hobo," 3450 m, 9 Aug 1914, *W. Limpricht 2169* (holotype: WRSL-not seen, photo and fragment-A image; isotypes: WRSL not seen, photo and fragment-E image, WU image).

Aster ramsbottomii Hand.-Mazz., J. Bot. (Brit. Foreign) 76: 284. 1938. **TYPE**: **CHINA**. **Xizang** (Tibet). Charndo district, Salween Gorge, 9000-10,000 ft, undershrub under a foot in height, sometimes a yard across, bearing a hundred or more flowers, … on the dry gravel or earth slopes, on cliffs, abundant throughout the arid region, 3 Aug 1933, *F. Kingdon-Ward 10675* (holotype: BM image-Fig. 16; isotype: E image-Fig. 17).

Gansu, Qinghai, Shaanxi, Sichuan, Xizang. Figure 13, in situ.

2. Sinobouffordia sikuensis (Smith & Farrer) Nesom, **comb. nov.** *Aster sikuensis* W.W. Smith & Farrer, Notes Roy. Bot. Gard. Edinburgh. 9: 80. 1916. **TYPE**: **CHINA**. **Gansu**. Stony places and hot banks about Siku, Kansu, Oct 1914, *F. Farrer and W. Purdom 456* (holotype: E 385637 image-Fig. 18; isotypes: E image-Fig. 19, E image-Fig. 20, MO image).

Gansu (the type), Shaanxi (voucher for Li et al. 2011), Sichuan (as cited by Chen et al. 2011).

Aster sikuensis was compared by Smith and Farrer in the protologue to *Aster holophyllus* (= *Aster pekinensis* = *Kalimeris integrifolia*), which is similar in aspect to *A. sikuensis* and also has glandular phyllaries and leaf surfaces and apically glandular achenes, but *A. pekinensis* is a taprooted, herbaceous perennial and part of the Kalimeris group morphologically (Gu & Hoch 1997) as well as molecularly (Li et al. 2012).

Online specimen images at PE identified as *Aster sikuensis* (via Chinese Virtual Herbarium 2020 — *Wang 7966*, *Fu 2127*, and *Y.Q. He 880*-2 sheets, from Gansu and Sichuan) (*Yeqi 880* annotated as such by Ling) are perennial herbs and apparently are some other species even though similar in aspect to *A. sikuensis*. Other collections in the Chinese Virtual Herbarium identified as *A. sikuensis* (all from WUK, none with images) are from Gansu, Shaanxi, and Sichuan.

The plant illustrated by Ling (1985) as representative of *Aster sikuensis* (his Fig. 2, p. 152; reproduced in Chen et al. 2001 as Fig. 518) has a base clearly drawn from *Wang 7956* (PE), which perhaps accounts for disparities between Flora of China descriptions and plants of the *A. sikuensis* type. The voucher of *A. sikuensis* for the molecular analysis (Li et al. 2001) was collected in Shaanxi (LWP0510025, Lueyang County).

Figure 13. *Sinobouffordia poliothamnus*. Top: Northwestern Sichuan, 30 July 2005. Bottom: Southeastern Xizang (Tibet), 21 July 2009. Photos (from color transparencies) by David Boufford, "Biodiversity of the Hengduan Mountains and adjacent areas of south-central China" website.

Figure 14. *Sinobouffordia poliothamnus*. Detail from *Aster ramsbottomii* holotype (BM).

Figure 15. *Sinobouffordia sikuensis*. Detail from *Aster sikuensis* holotype (E).

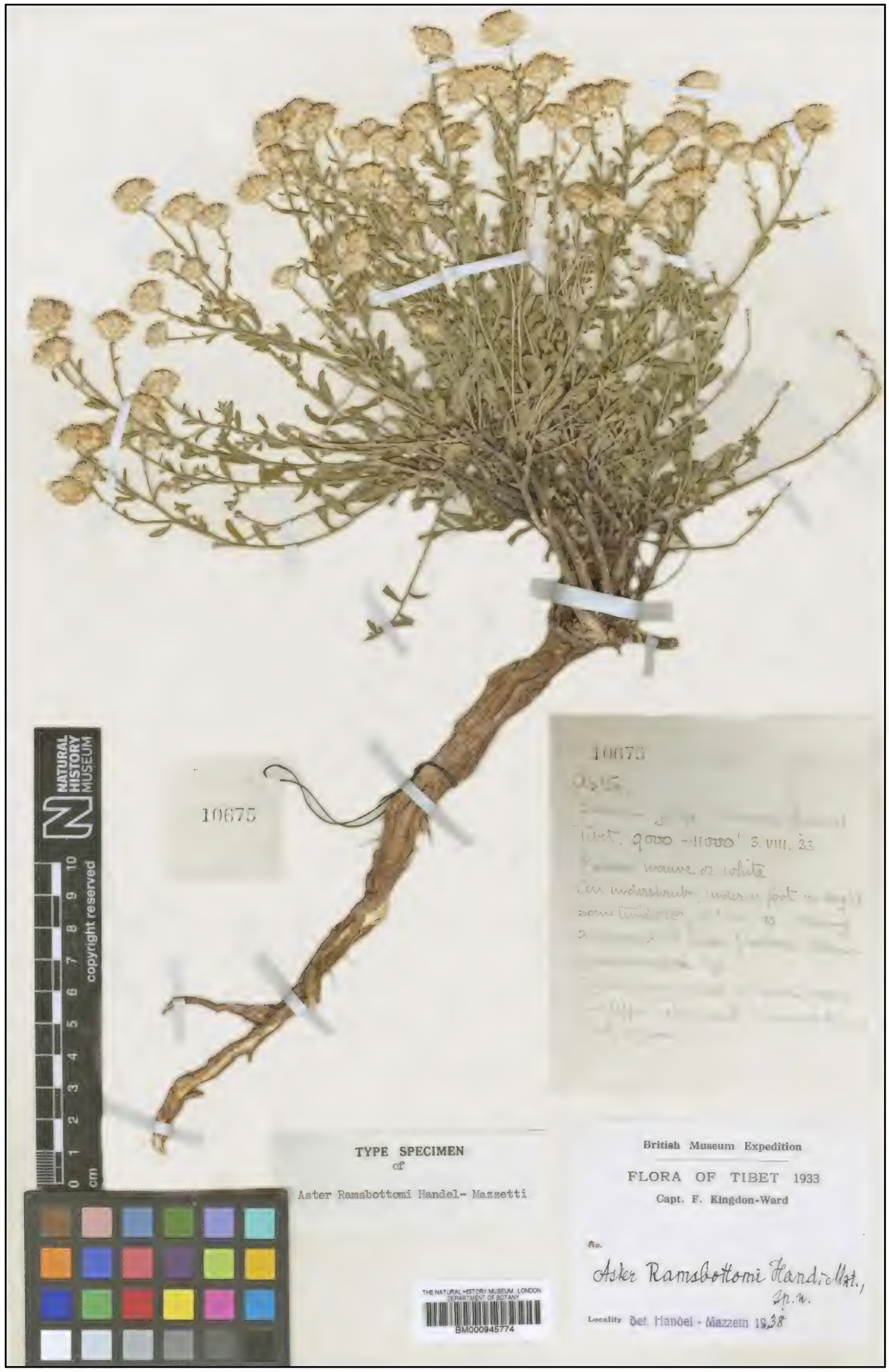

Figure 16. *Sinobouffordia poliothamnus*. Holotype of *Aster ramsbottomii* (BM).

Figure 17. *Sinobouffordia poliothamnus*. Isotype of *Aster ramsbottomii* (E).

Figure 18. *Sinobouffordia sikuensis*. Holotype of *Aster sikuensis* (E).

Figure 19. *Sinobouffordia sikuensis*. Isotype of *Aster sikuensis* (E).

Figure 20. *Sinobouffordia sikuensis*. Isotype of *Aster sikuensis* (E).

ACKNOWLEDGEMENTS

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METAMYRIACTIS (ASTERACEAE, ASTEREAE), A NEW GENUS OF SOUTHEAST ASIAN ASTERS

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ABSTRACT

Metamyriactis Nesom, **gen. nov.**, segregated from *Aster*, includes 5 species: ***Metamyriactis helenae*** (Merrill) Nesom, **comb. nov.**, ***Metamyriactis nigromontana*** (Dunn) Nesom, **comb. nov.**, ***Metamyriactis pandurata*** (Nees ex Walpers) Nesom, **comb. nov.**, ***Metamyriactis pycnophylla*** (Franch. ex W.W. Smith) Nesom, **comb. nov.**, ***Metamyriactis sikkimensis*** (Hook. f.) Nesom, **comb. nov.**, and ***Metamyriactis veitchiana*** (Hutch. & Drummond ex Zhang & Gao) Nesom, **comb. nov.** *Metamyriactis pandurata* is common and widespread at low to medium elevations in central China, while the others are mostly Himalayan at higher elevations. The genus is characterized particularly by a herbaceous-rhizomatous habit, zig-zag stems, clasping to subclasping leaf bases, minutely glandular stems, leaves, and disc corollas, and small, narrowly obovate, densely glandular achenes. Phylogenetic analyses based on molecular data indicate that *M. pandurata* and *M. pycnophylla* are closely related to each other and as a pair most closely related to *Myriactis*. Lectotypes are designated for *Aster fordii*, *Aster candelabrum*, *Aster sikkimensis*, and *Erigeron panduratus*.

Molecular analyses (Li et al. 2012) indicate that the Chinese taxa *Aster auriculatus*, *A. panduratus*, and *A. pycnophyllus* are closely related among themselves and as a group most closely related to the genus *Myriactis*. This group of species is part of a clade that includes *Psychrogeton*, *Neobrachyactis*, *Callistephus*, and six other species groups recognized at generic rank (Nesom 2020a).

Not only is the association of *Myriactis* with *Aster* unexpected but also the morphological distance between *Aster auriculatus*/*panduratus* and *A. pycnophyllus* has not previously led to a hypothesis of their close relationship. Grierson (1964), however, pointed to a close morphological relationship among *Aster pycnophyllus*, *A. helenae*, *A. nigromontanus*, and *A. sikkimensis*, noting (p. 112) that "they all have flexuose [zig-zag] stems, distinctly veined leaves, and ligules that have two well-marked lateral veins." Similarity of *A. nigromontanus* and *A. sikkimensis* to *A. auriculatus*/*panduratus* links the latter to this group. These three have essentially sessile leaves, often with a clasping to subclasping base, while leaves of *A. pycnophyllus* and *A. helenae* have truncate to rounded-obtuse blade bases but are distinctly petiolate. Ling (1985) included *A. pycnophyllus* with *A. nigromontanus* and *A. sikkimensis* as the members of his ser. *Sikkimenses*. His ser. *Auriculati* included *A. auriculatus*, *A. panduratus*, and *A. sphaerotus* (representing a single variable and widespread species, as recognized here) and *A. veitchianus* (a distinct, narrowly endemic species).

In any case, this group of species can be recognized as a natural group among Asian asters, especially in their combination of herbaceous and rhizomatous habit, zig-zag stems, pervasive glandularity, relatively small heads and short rays, foveolate to alveolate receptacles, and small, compressed, glandular achenes. They are treated here at generic rank as the new genus *Metamyriactis*, with recognition from molecular evidence that they apparently are the sister genus of *Myriactis* (one other genus, the Hawaiian *Helodeaster*, is closely related to *Myriactis*; see Nesom 2020b).

In his *Aster* ser. *Auriculati*, Ling (1985) also included *A. trichoneurus* and *A. manshanensis*. Leaf and involucral morphology of these, however, suggest they are closer to *A. sampsonii* and *A. maackii* of the Amellus group of Asterinae (Nesom 2020a).

Aster alatipes Hemsl. (Figs. 30-32) has clasping leaf bases, glandular stems, leaves, involucres and disc corollas, and small, glandular achenes and might be suspected of close relationship with *Metamyriactis pandurata*, but the involucral morphology of *A. alatipes* (phyllaries strongly scarious-indurate, graduate in length, oblong-elliptic with rounded apices) is distinct from that of the species placed here in *Metamyriactis*.

METAMYRIACTIS Nesom, **gen. nov.** **TYPE**: **Metamyriactis pycnophylla** (Franch. ex W.W. Smith) Nesom

Aster [sect. *Aster*] ser. *Auriculati* Y. Ling, Fl. Reipubl. Pop. Sin. 74: 358. 1985. **TYPE**: *Aster auriculatus* Franch.

Aster [sect. *Orthomeris*] ser. *Sikkimenses* Y. Ling, Fl. Reipubl. Pop. Sin. 74: 358. 1985. **TYPE**: *Aster sikkimensis* Hook. f.

Distinct among Asian asters in the combination of its rhizomatous habit, zig-zag stems, stems, leaves, phyllaries, and disc corollas minutely glandular, leaves epetiolate or with a broadly winged petiole and clasping base (*M. pandurata*, *M. veitchiana*, *M. nigromontana*, *M. sikkimensis*) or distinctly short-petiolate (*M. pycnophylla*, *M. helenae*), relatively small heads and short rays, foveolate to alveolate receptacles, and narrowly oblanceolate achenes 1.8–3 mm long, strongly compressed, 2(–4)-ribbed, strigose and minutely stipitate-glandular.

Perennial herbs from a short, thick, fibrous-rooted rhizome/caudex and longer, thinner rhizomes or (in *M. pandurata*) stolons up to 15 cm long; stems, leaves, and phyllaries stipitate-glandular to punctate-glandular, moderately to densely hirsute-villous. **Stems** (5–)20–80(–100) cm tall, simple, distally branching, zig-zag at nodes, sometimes proximally lignescent (*M. nigromontana*, *M. sikkimensis*). **Leaves** , proximal small and withered by anthesis, epetiolate or with a broadly winged petiole, clasping to subclasping. **Heads** 1 or usually in loose to dense corymboid clusters; involucres shallowly hemispheric, 4–12 mm wide (pressed); phyllaries in 3–4 subsequal series, mostly herbaceous, apically acute to acuminate; receptacles epaleate, foveolate to alveolate. **Ray flowers** (10–)20–60, ligules 4–9(–10) mm long, white to blue or purple. **Disc flowers** bisexual, fertile, corollas 3.5–5 mm long, sometimes becoming purple, tube filiform, abruptly expanded into the limb, lobes triangular-deltate, often glandular. **Achenes** narrowly obovate, 1.8–3 mm long, strongly compressed, 2(–4)-ribbed, strigose and minutely stipitate-glandular apically or over the whole surface; pappus of bristles in 3–4 series of subequal length, often reddish, innermost about as long as the disc corollas, apically acute or slightly clavate, outermost much shorter, 0.2–0.6 mm long.

1. Leaves with a narrow, clearly delimited petiole; involucres 4–6 mm wide (pressed).
   2. Internodes 25–45 mm long; distal leaves narrowly ovate, base rounded to obtuse; Xizang, Yunnan, Assam, n Myanmar ..... **Metamyriactis pycnophylla**
   2. Internodes 4–10 mm long; distal leaves lanceolate, base attenuate; ne Myanmar ..... **Metamyriactis helenae**

1. Leaves essentially sessile (sometimes short-petiolate in *M. sikkimensis*), with a truncate to rounded or obtuse base; involucres 6–12 mm wide (pressed).
   3. Cauline leaves mostly 10–18 cm long, distal only slightly reduced in size, not bracteate; rays usually blue to pink or purple; involucres 6–8 mm wide (pressed).
      4. Longest phyllaries 5–5.5 mm long; disc corollas 5 mm long; ray flowers 20–30; Yunnan ..... **Metamyriactis nigromontana**
      4. Longest phyllaries 3.5–4 mm long; disc corollas 3.5-4 mm long; ray flowers 30–60; Sikkim, Nepal, s Xizang ..... **Metamyriactis sikkimensis**
   3. Cauline leaves mostly 3–8 cm long, distal absent or much-reduced and becoming bracteate; rays white to light pink, light blue, or light purple; involucres 10–12 mm wide (pressed).

5. Cauline leaves more than 15, basal withered by anthesis; abaxial leaf surface glandular; heads (1–)3–30; phyllaries glandular; widespread in China (see below) ..... **Metamyriactis pandurata**

5. Cauline leaves usually fewer than 10, basal present at anthesis; abaxial leaf surface without glands; heads 1–4; phyllaries glabrous; endemic to E'mei and Yinjin counties, Sichuan ..... **Metamyriactis veitchiana**

1. **Metamyriactis pycnophylla** (Franch. ex W.W. Smith) Nesom, **comb. nov.** *Aster pycnophyllus* Franch. ex W.W. Smith, Notes Roy. Bot. Gard. Edinb. 8: 332. 1915. *Aster harrowianus* var. *pycnophyllus* (Franch. ex W.W. Sm.) H. Lév., Cat. Pl. Yun-Nan, 40. 1915. **TYPE**: **CHINA**. **Yunnan**. Tali Range eastern flank, 25° 40' N, shady ledges of cliffs in side valleys, 10,000-11,000 ft, Sept 1906, *G. Forrest 4001* (holotype: E image, Fig. 1). Figs. 1-5.

2. **Metamyriactis helenae** (Merrill) Nesom, **comb. nov.** *Aster helenae* Merrill, Brittonia 4: 185. 1941. **TYPE**: **MYANMAR**. N Burma, Kang-fang, amongst mossy stones on the fringe of forest lining the river, at just about the high water mark, 5500 ft, 5 Dec 1938, *F.K. Ward 81* (holotype: NY image, Fig. 6).

3. **Metamyriactis pandurata** (Nees ex Walpers) Nesom, **comb. nov.** *Aster panduratus* Nees ex Walpers, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19 (Suppl. 1): 258. 1843. **TYPE**: **CHINA**. [**Guangdong**]. "Lintin" [= Nei/Inner Lingding Island], [1831], *F.J.F. Meyen s.n.* (B, not seen). Figs. 7-19.

Merrill (1937, p. 74) noted that "Doctor Mattfeld examined Nees' type in the Berlin Herbarium and states that it represents the same species as Hongkong herb. 2824, distributed as *A. Fordii* Hemsl."

Aster striatus Champion in Benth., Hooker's J. Bot. 4: 233. 1852. **TYPE**: **CHINA**. **Guangdong**. Hong-kong, [no date], *J.G. Champion s.n.* (holotype: K image).

Aster fordii Hemsl., J. Linn. Soc., Bot. 23: 410. 1888. **LECTOTYPE** (designated here): **CHINA**. **Guangdong**. "Lo Fau Shan: Com. Hort Bot. Hongkong 11/83," 800 ft, Aug 1883, *C. Ford 88* (K image). Also cited in the protologue: "Hupeh: *A. Henry 984*, *2494*, *2910*, *3229*."

Aster auriculatus Franch., J. Bot. (Morot). 10: 376. 1896. **TYPE**: **CHINA**. **Yunnan**. In collibus, ad imam basin montis Tsang-chan, 13 Jun 1889, *P.J.M. Delavay 4157* (holotype: P, photo and fragments-E image).

Aster candelabrum Vaniot, Bull. Acad. Int. Géogr. Bot. 12(167–168): 498. 1903. **TYPE**: **CHINA**. [**Guizhou**.] Prov. Kouy-tchéou, environs de Kouy-Yang, sur les montagnes du collège, 30 Aug 1897, *E. Bodinier 1915* (holotype: E 413431 image). Protologue: "Chine, Kouy-tchéou; environs de Kouy-Yang. C. sur les montagnes du collège. *Item*, aux environs de Gan-pin. Léon Martin legit, 30 août 1897. Herbier Bodinier, no. 1915." The protologue appears to refer to two collections but the wording is repeated on the label of the type, added in a different-colored ink to the original information and also with the addition of "L. Martin" as collector. Thus it is clear enough that the protologue refers only to the single sheet and that Bodinier made the collection.

Aster argyi H. Lév., Bull. Géogr. Bot. 25: 14. 1915. **TYPE**: **CHINA**. **Jiangsu**. "Kiang-Sou, Wousi-Long-Tse," [no date], *Père C. d'Argy s.n.* (holotype: E image).

Erigeron panduratus C.-C. Chang, Sunyatsenia 6: 17. 1941 (not *Aster panduratus* Nees ex Walpers 1843). *Aster sphaerotus* Y. Ling [nom. nov.], Fl. Reipubl. Pop. Sin. 74: 145. 1985. **LECTOTYPE** (designated here): **CHINA**. **Guangxi**. "Tze-Yuen Hsien, Mao-Er Shan, herb in woods," 28 Jul 1937, *Z.S. Chung 83430* (IBK 191566 image; isolectotypes: A image, Fig. 10, IBK 191567 image).

Leaves cauline, gradually becoming larger distally, largest at midstem or above, becoming bracteate in the inflorescence, broadly oblanceolate to oblong-oblanceolate, mostly 3–8 cm long, 1–2.5 cm wide, base cordate or auriculate, sessile and clasping to subclasping, margins entire to serrate or dentate, sometimes coarsely so, apex acute to obtuse. **Heads** 1 or 2–10(–30) in loose clusters. **Involucres** 10–12 mm wide (pressed), phyllaries oblong-lanceolate to elliptic-lanceolate, apex acuminate or abruptly narrowed, minutely stipitate-glandular, stramineous with a dark midvein, outermost with broader midvein or midregion. **Ray flowers** 18–30(–40), ligules 5–9 mm long, white to light pink or light blue or purple. **Achenes** 1.8–3 mm long; pappus bristles 4–5 mm long. $2n$=18 (Meng et al. 2016).

Open forests, mixed forests, thickets, grasslands on slopes, canal sides, roadsides, field margins; 100–3000 meters. **China**: Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hubei, Henan, Jiangsu, Jiangxi, Sichuan, Zhejiang, Xizang (Zayü), Yunnan; apparently adentive in **Thailand** (fide Kew*science*, Plants of the World Online).

There is little difference in the morphological descriptions of *Aster auriculatus*, *A. panduratus*, and *A. sphaerotus* in the treatment of *Aster* for the Flora of China (Chen et al. 2011, following Ling 1985) and their geographical distributions as summarized in FOC are overlapping. The type of *Aster sphaerotus* has a different aspect, perhaps in part because of anthocyanin development (Fig. 4), but it is within the morphological range of *A. panduratus*/*auriculatus*. Observations here do not corroborate putative distinctions in involucre and achene size between *A. sphaerotus* and the others (see details with ruler in Figs. 10, 11, and 19). These taxa were separated in the FOC by contrasts in the key below.

a. Phyllaries 2–3-seriate, subequal, outer usually leaflike; rays white ..... *Aster auriculatus*
a. Phyllaries 3–4 seriate, unequal, leaflike in upper part; rays blue or purple.

b. Involucres 7–8(–10) mm; achenes 2.7 mm or more ..... *Aster sphaerotus*
b. Involucres ca. 5 mm; achenes ca. 1.5 mm ..... *Aster panduratus*

Among these three (and other synonyms), only a single, widespread species is recognized here, with variability shown in Figs. 6-18.

4. Metamyriactis veitchiana (Hutch. & Drummond ex Zhang & Gao) Nesom, **comb. nov.** *Aster veitchianus* Hutch. & Drummond ex Zhang & Gao, Phytotaxa 152: 53. 2013. **TYPE**: **CHINA**. **Sichuan**. Mt. E'mei, Qingyingge, 950 m, 8 Jun 1933, *X.B. Peng 6049* (holotype: PE, image in Zhang et al. 2013; isotype: IBK image, Fig. 20). See Zhang et al. (2013) for detailed comments on nomenclature. Figs. 19-21.

5. Metamyriactis nigromontana (Dunn) Nesom, **comb. nov.** *Aster nigromontanus* Dunn, J. Linn. Soc., Bot. 35: 501. 1903. **TYPE**: **CHINA**. **Yunnan**. Mengtze, N Mts, 8000 ft, *A. Henry 11302* (holotype: K presumably, not seen; isotypes: E image-Fig. 22, MO image). Protologue: "Obtained by Henry's native collector Ho on the summit of Great Black Mountain at 8000 ft. near Mengtze." Figs. 23-24.

6. Metamyriactis sikkimensis (Hook. f.) Nesom, **comb. nov.** *Aster sikkimensis* Hook. f., Curtis's Bot. Mag. 77: t. 4557. 1851. **LECTOTYPE** (designated here): **INDIA**. **Sikkim**. Singalelah, [ca. 21 May 1848, fide Hooker's Himalayan Journal], *J.D. Hooker s.n.* (K 102210 image, Fig. 24; possible isolectotypes: E, BM, K-many, L, M, MPU, P-2 sheets — images of all). All of the sheets distributed outside of K have the printed label with only Sikkim as locality, but Hooker collected the species at "Chola, 9000 ft" and Lachoong, 10,000 ft" (see Fig. 25) as well as at Singalelah (the lectotype), so the provenance of the "possible isolectotypes" is unknown. Figs. 25-29.

In the Flora of British India, J.D. Hooker (1881) attributed authorship of the species to "Hook. f. & Thoms.," crediting himself and his Himalayan collecting companion, but there is no mention of Thomson

in the protologue and "W.J.H." (W.J. Hooker) is credited as supplying the protologue's technical description. The protologue, written by John Smith (except for Hooker's description), notes that plants were "Raised from seeds sent by Dr. Hooker to the Royal Gardens of Kew from the alpine regions of Sikkim." Grierson (1964) cited cultivated specimens ("Hort. Kew, 1851, (syntype K, E))," but images of these apparently are not online and, although no collections were cited in the protologue, it is assumed here that Hooker intended his Sikkim collections as type material. It is assumed here, but not with certainty, that Smith's attribution of the protologue description to W.J. Hooker rather than to J.D. Hooker was in error.

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Figure 1. *Metamyriactis pycnophylla*. Yunnan, holotype (E).

Figure 2. *Metamyriactis pycnophylla*. Along the Myanmar-Yunnan border, *Collector 1346* (E).

Figure 3. *Metamyriactis pycnophylla*. Yunnan, *McLarin 235* (E).

Nesom: *Metamyriactis*, gen. nov.

Figure 4. *Metamyriactis pycnophylla*. Yunnan, *Rock 7615* (US).

Nesom: *Metamyriactis*, gen. nov.

Figure 5. *Metamyriactis pycnophylla*. Yunnan, *Forrest 16108* (E).

Figure 6. *Metamyriactis helenae*. Myanmar, holotype (NY).

Figure 7. *Metamyriactis pandurata*. HongKong Herbarium <https://www.herbarium.gov.hk/>

Figure 8. *Metamyriactis pandurata*. HongKong Herbarium <https://www.herbarium.gov.hk/>

Figure 9. *Metamyriactis pandurata*. Photo by 翁明毅, 2012, "Leaves of Flora in Taiwan" folder, Flickr.

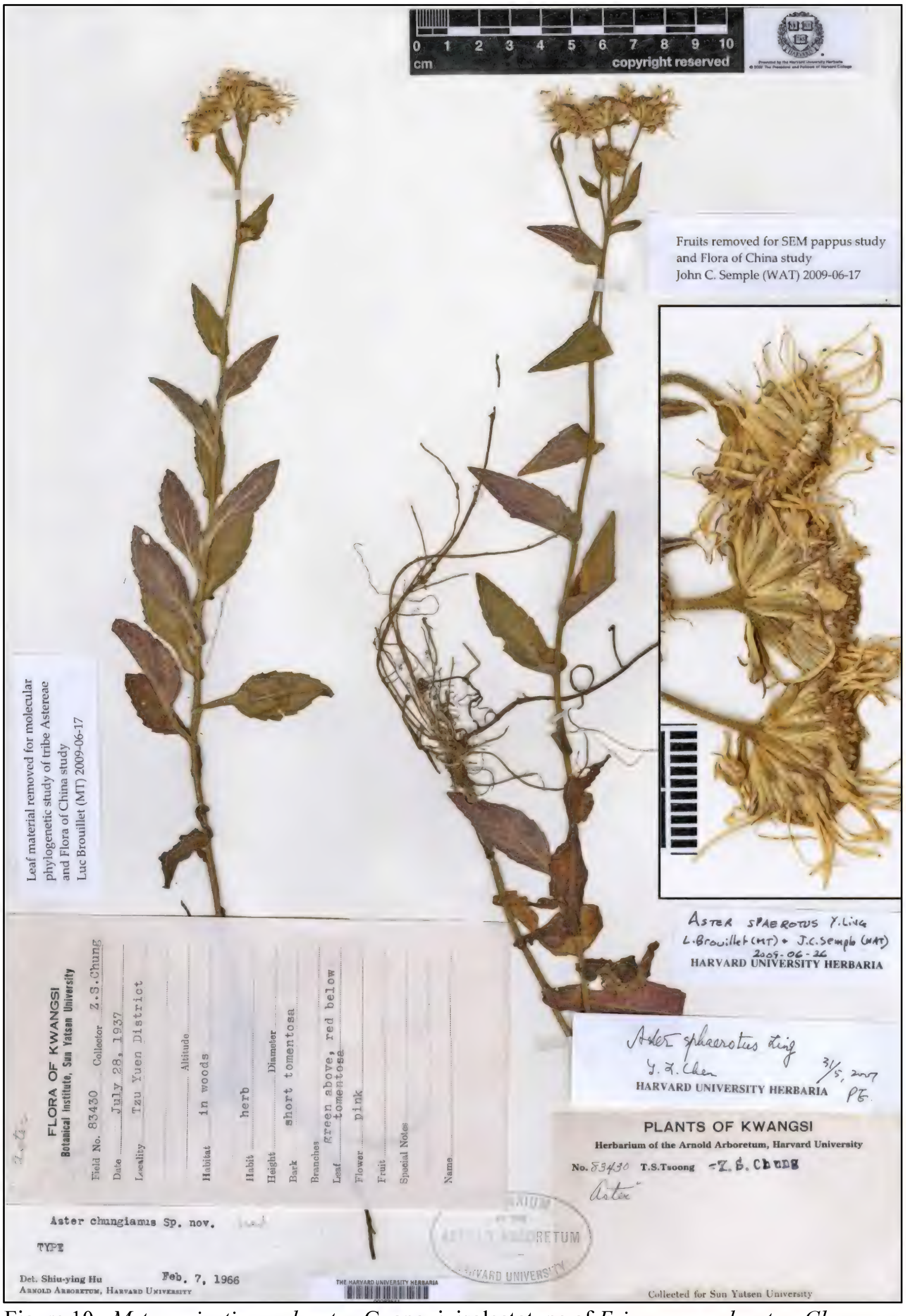

Figure 10. *Metamyriactis pandurata*. Guangxi, isolectotype of *Erigeron panduratus*, *Chung 83430* (A).

Figure 11. *Metamyriactis pandurata*. Yunnan, *Rock 9038* (US).

Figure 12. *Metamyriactis pandurata*. Zhejiang, *Ching 9087* (US).

Figure 13. *Metamyriactis pandurata*. Guangdong, *Hu 5684* (US).

Nesom: *Metamyriactis*, gen. nov.

Figure 14 *Metamyriactis pandurata*. Fujian, *Norton 1443* (US).

Nesom: *Metamyriactis*, gen. nov.

Figure 15. *Metamyriactis pandurata*. Yunnan, *Yu 19116* (E).

Figure 16. *Metamyriactis pandurata*. Yunnan, *Sino-British Expedition 1136* (E).

Figure 17. *Metamyriactis pandurata*. Guizhou, *Teng 90337* (L).

Figure 18. *Metamyriactis pandurata*. Guangdong, *Hu 12227* (US).

Figure 19. *Metamyriactis pandurata*. Yunnan, *Henry 9445A* (US).

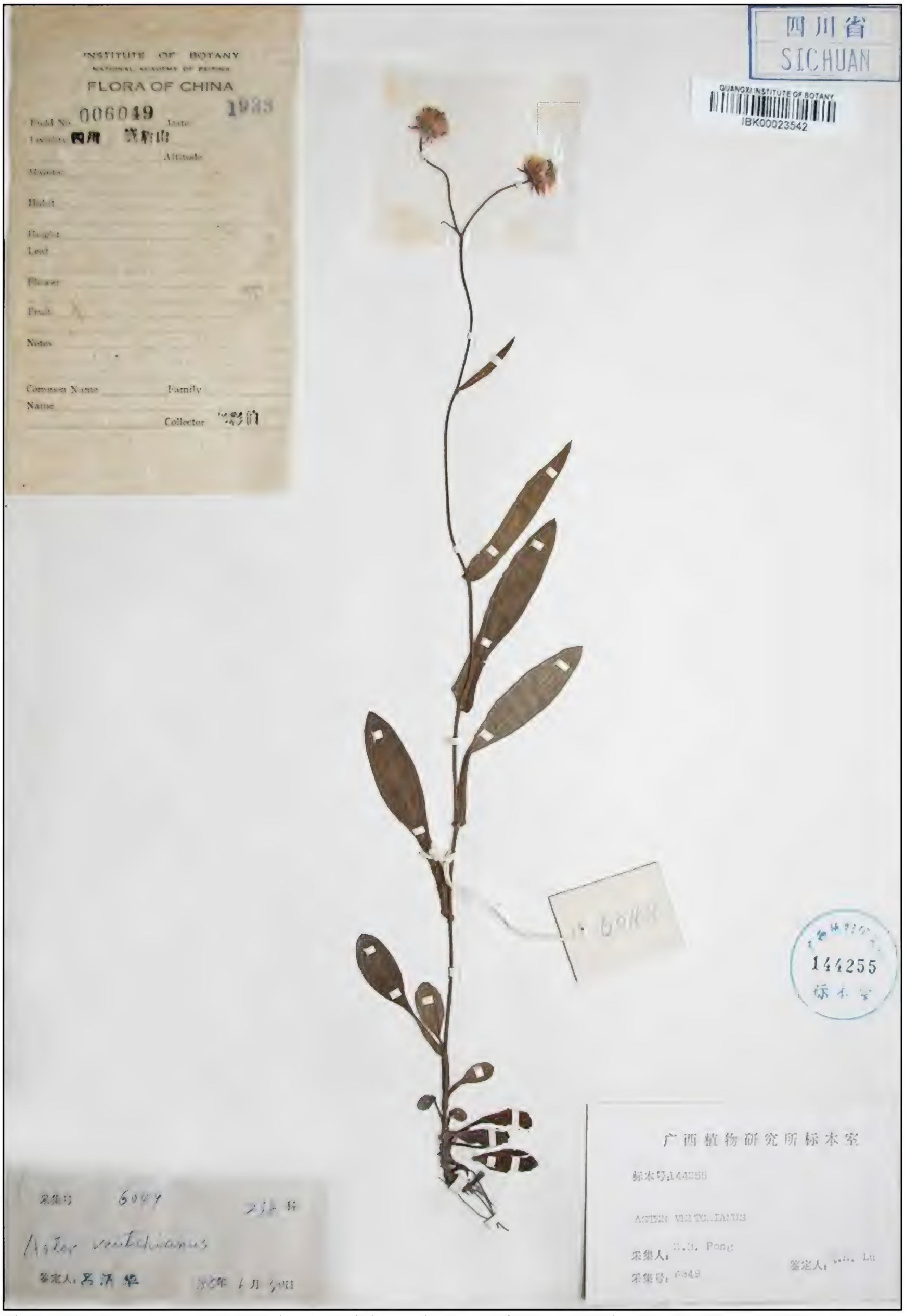

Figure 20. *Metamyriactis veitchiana*. Sichuan, isotype of *Aster veitchianus* (IBK).

Figure 21. *Metamyriactis veitchiana*. Sichuan, *Yang 54953* (IBSC).

Figure 22. *Metamyriactis veitchiana*. Sichuan, *Fang 11857* (IBSC).

Figure 23. *Metamyriactis nigromontana*. Yunnan, isotype (E).

Figure 24. *Metamyriactis nigromontana*. Yunnan (PE).

Figure 25. *Metamyriactis sikkimensis*. Sikkim, lectotype (K).

Figure 26. *Metamyriactis sikkimensis*. Sikkim (Lachoong, right; Chola, left), *Hooker s.n.* (K).

Figure 27. *Metamyriactis sikkimensis*. Sikkim (sw of Lachung), *Ribu & Rhomoo 6711* (E).

Figure 28. *Metamyriactis sikkimensis*. Langtang, Sikkim. Photo by David Ritscher, Oct 2019, iNaturalist.

Figure 29. *Metamyriactis sikkimensis*. Langtang, Sikkim. Photo by David Ritscher, 16 Oct 2019, iNaturalist.

Figure 30. *Aster alatipes*. Holotype (K).

Figure 31. *Aster alatipes*. Isotype (GH).

Figure 32. *Aster alatipes*. From the holotype.

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CHLAMYDITES (ASTERACEAE: ASTEREAE) REVIVED

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ABSTRACT

Chlamydites J.R. Drummond of the Tibetan Plateau has included a single species, *C. prainii* J.R. Drummond (= *Aster prainii*). *Wardaster lanuginosus* (= *Aster neolanuginosus*) is regarded here a synonym, as is the Tibetan *Aster hololachnus*, and all are treated as monotypic *Chlamydites*. A lectotype is designated for *A. prainii*. *Aster prainii* has not been included in molecular-phylogenetic analyses but it is hypothesized here to have arisen evolutionarily from near the ancestors of *Aster flaccidus* and *Aster batangensis*.

The dense, white, lanate-villous vestiture of a Himalayan alpine species impressed both J.R. Drummond (1907) and J. Small (1926) to the extent that each, independently, described it as a new species and placed it in a new genus. Emphasizing the hairy disc corollas, Drummond considered his *Chlamydites prainii* to be closely related to the Andean genus *Werneria* or at least to species of Senecioneae. Small recognized the similarity of *Wardaster lanuginosus* to monocephalous alpine species of *Aster* but noted that it differs in its alveolate receptacle and "mucronate anthers." Ling (1985) and Chen et al. (2011) included both among the species of Chinese *Aster* (as *Aster prainii* and *Aster neolanuginosus*).

Aster hololachnus Y. Ling, another densely lanate-villous alpine species similar in its caespitose, monocephalous habit to *A. prainii* and *A. neolanuginosus*, was compared in the protologue to *A. flaccidus*, differing from the latter its vestiture and narrower phyllaries and ray florets. Ling (1985) placed *Aster prainii* and *A. lanuginosus* as *Aster* ser. *Prainiani* but included *A. hololachnus* among species of his ser. *Asteroides*, which also included *A. asteroides*, *A. likiangensis*, *A. flaccidus*, and *A. tsarungensis*. Ling's protologue comparison to *A. flaccidus* was essentially repeated in the entry for *A. hololachnus* by Chen et al. (2011), with no mention of similarity to *A. prainii* or *A. neolanuginosus*.

Aster flaccidus does not form caespitose mats, it is distinct in involucral morphology, and it produces long ray styles characteristic of the newly described genus *Tibetiodes* (Nesom 2020a, 2020b). The Flora of China illustration of *A. prainii* (Ling 1985; Chen et al. 2011) shows the ray style barely extending beyond the corolla tube.

The key of Chen et al. separates *Aster prainii*, *A. neolanuginosus*, and *A. hololachnus* as follows:

a. Pappus 3- or 4-seriate ..... 112. **Aster hololachnus**
a. Pappus 2–4-seriate.
b. Disk corolla tube and limb sparsely villosulous, lobes lanate ..... 107. **A. prainii**
b. Disk corolla tube and limb without long hairs ..... 108. **A. neolanuginosus**

In view of their otherwise strong similarity, these putative differences need to be verified. The difference in involucral morphology does not provide an objective choice and I have not been able to see details of corolla vestiture. *Aster prainii*, *A. neolanuginosus*, and *A. hololachnus* are treated here a single species, emphasizing their unusual habit and vestiture and the apparently compact geography of the populations in Bhutan, southeastern Tibet, and western and southwestern Sichuan. Consistent differences may prove to exist and support a less conservative taxonomy.

The white-lanate taxa key in the Flora of China (Chen et al. 2011) among the species of *Aster* sect. *Alpigeni* because of their basal rosette, solitary heads, and subequal-length phyllaries, but *A. prainii* appears to be morphologically isolated among Asian species, both in its vestiture and extensive system of rhizomes (producing plants in colonial mats). *Aster prainii* has not been included in molecular phylogenetic analyses — its evolutionary position in the Psychrogeton branch of Asterinae (Nesom 2020a) is speculative.

Aster batangensis (= *Geothamnus*; Nesom 2020c) is monocephalous and mat-forming in habit similar to *A. prainii* but differs in its glabrate to sparsely hirsute-strigose vestiture. Its underground system is essentially a branching caudex, the branches woody and often with prominent secondary growth.

CHLAMYDITES J.R. Drummond, Bull. Misc. Inform. Kew 1907: 91. 1907. **TYPE**: *Chlamydites prainii* J.R. Drummond

Wardaster J. Small, Trans. Proc. Bot. Soc. Edinburgh 29: 230. 1926. **TYPE**: *Wardaster lanuginosus* J. Small

Aster sect. *Alpigenia* ser. *Prainiani* Ling, Fl. Reipubl. Popularis Sin. 74 (Addendum): 360. 1985. **TYPE**: *Aster prainii* (J.R. Drummond) Y.L. Chen

Perennial herbs, caespitose and mat-forming from a system of branching, non-woody rhizomes; stems, leaves, and involucres tomentose to white-lanate, glandular beneath the tomentum. **Stems** 3–15 cm high, unbranched. **Leaves** basal and cauline, basal in persistent rosettes, spatulate to oblanceolate, margins entire, cauline reduced in size, lanceolate to oblanceolate, not clasping. **Heads** terminal, solitary. **Involucres** broadly campanulate, (15– in *Aster hololachnus*) 24–28 mm wide (pressed); phyllaries 1–2-seriate, subequal, herbaceous, linear-oblong and apically acute, longer than the disc corollas, sometimes loose and spreading; receptacles alveolate. **Ray flowers** 20–50, ligules blue to pinkish, purple, or violet, ligules 10–16 mm long, coiling. **Disc flowers** bisexual, fertile; corollas 6–7 mm long, lobes triangular, erect (without or without hairs, glandular or eglandular); anther thecae without tails, apical appendages broadly lanceolate and prominent. **Achenes** narrowly obovoid, compressed, ca. 3 mm long, 2–4-ribbed, strigose-sericeous, eglandular; pappus of barbellate bristles of unequal length, longest equalling or slightly longer than the disc corollas, innermost weakly clavate apically, outermost series of scales 0.5–1 mm.

1. Chlamydites prainii J.R. Drummond, Bull. Misc. Inform. Kew 1907: 91. 1907. *Aster prainii* (J.R. Drummond) Y.L. Chen, Geol. Ecol. Stud. Qinghai-Xizang Plateau 2: 1314. 1981. **LECTOTYPE** (designated here): **CHINA**. **Xizang**. Kambajong [Khamber Jong], Sep 1903, *Maj. D. Prain s.n.* (BM image, Figs. 1, 2). The protologue also cited *Walton s.n.* (not seen), Aug 1904, from Lhasa.

Wardaster lanuginosus J. Small, Trans. Proc. Bot. Soc. Edinb. 29: 230. 1926. *Aster lanuginosus* (J. Small) Y. Ling in Y. Ling & Y.L. Chen, Fl. Reipubl. Popularis Sin. 74: 234. 1985 [not *Aster lanuginosus* H.L. Wendland in Bartling & Wendland, Beitr. Bot. 2: 9. 1825]. *Aster neolanuginosus* Brouillet, Semple, & Y.L. Chen [nom. nov.], Fl. China 20-21: 625. 2011. **TYPE**: **CHINA**. [**Sichuan**]. West China, Glacier Lake Camp, 28° 5' N, 100° 45' E (W of Muli), high cliffs and boulder screes of slate, 15,000 ft, *F. Kingdon-Ward 4686* (holotype: E image, Fig. 3).

Aster hololachnus Y. Ling ex Y.L. Chen et al., Acta Phytotax. Sin. 19: 88. 1981. **TYPE**: **CHINA**. **Xizang**. Qomolangma [Mt. Everest], Main Rongbuk Glacier, 5350 m, 7 Sep 1959, *Exped. ad montem Qomolangma 640* (holotype: PE image, Fig. 4).

Rocky slopes above snowline, glacier areas; 4200–5400 m. Bhutan, southeastern Tibet (Xizang), western and southwestern Sichuan. Figures 1–12.

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Figure 1. *Chlamydites prainii*. Tibet. Lectotype of *Chlamydites prainii* (BM).

Figure 2. *Chlamydites prainii*. Detail from Fig. 1, lectotype of *Chlamydites prainii.*

Figure 3. *Chlamydites prainii*. Southwestern Sichuan. Holotype of *Wardaster lanuginosus* (E).

Figure 4. *Chlamydites prainii*. Tibet, Mt. Everest region. Holotype of *Aster hololachnus* (PE).

Figure 5. *Chlamydites prainii*. Tibet. *Sino-Japanese expedition team T691* (PE).

Figure 6. *Chlamydites prainii*. Tibet, Near Lhasa. *Ludlow & Sherriff 8993* (E).

Figure 7. *Chlamydites prainii*. Tibet. *Zhang Yongtian Lang Kaiyong 2061* (PE 300201).

Figure 8. *Chlamydites prainii*. Tibet. *Zhang Yongtian Lang Kaiyong 2061* (PE 300202).

Figure 9. *Chlamydites prainii*. Bhutan, *Ludlow, Sherriff, & Hicks 19764* (E).

Figure 10. *Chlamydites prainii*. Western Sichuan, *Boufford et al. 42295* (P). See Figure 12.

Figure 11. *Chlamydites prainii*. Western Sichuan. Detail from Fig. 10, *Boufford et al. 42295* (P).

Figure 12. *Chlamydites prainii*. Western Sichuan, W of the city of Litang, ca. 4500 meters. Photo by Jipei YUE, 26 July 2010. Website: Biodiversity of the Hengduan Mountains and adjacent areas of south-central China. *Boufford et al. 42295* collected at this site (see Figs. 10, 11).

Nesom, G.L. 2020. *Cordiofontis* (Asteraceae: Astereae), a new genus of Himalayan species segregated from *Aster*. Phytoneuron 2020-60: 1-20. Published 19 August 2020. ISSN 2153 733X

CORDIOFONTIS (ASTERACEAE: ASTEREAE), A NEW GENUS OF HIMALAYAN SPECIES SEGREGATED FROM *ASTER*

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ABSTRACT

Five *Aster* species from the Himalayan region comprise **Cordiofontis** Nesom, **gen. nov.** — four from Pakistan to Nepal and one from adjacent China: ***Cordiofontis flexuosa*** (Royle ex Lindl.) Nesom, **comb. nov.**, ***Cordiofontis laka*** (C.B. Clarke) Nesom, **comb. nov.**, ***Cordiofontis longipetiolata*** (Y. Ling) Nesom, **comb. nov.**, ***Cordiofontis nepalensis*** (Grierson) Nesom, **comb. et stat. nov.**, and ***Cordiofontis peduncularis*** (Wall. ex Nees) Nesom, **comb. nov.** The genus is distinct in its rhizomatous-perennial, herbaceous habit, hairy but eglandular vestiture, mostly cordate-petiolate leaf blades with basally dilated-sheathing petioles, solitary or few heads on few-bracteate peduncles in a loose corymb, herbaceous outer phyllaries, fusiform and eglandular achenes, and biseriate pappus of acute-tipped bristles. Molecular data place *Cordiofontis* (represented so far in molecular sampling only by *C. longipetiolata*) in an unresolved position among species and species groups of the Psychrogeton branch of subtribe Asterinae. A key to the species, formal typification, and images of types and representative specimens are provided.

Molecular data of Li et al. (2012) and Farhani et al. (2018) place the Chinese species *Aster longipetiolatus* Y. Ling (= *Kalimeris longipetiolata*) in an unresolved position among species and species groups of the Psychrogeton branch of subtribe Asterinae (Nesom 2020a), which includes *Psychrogeton*, *Callistephus*, the *Aster diplostephioides* group (described in this series as the genus *Tibetiodes*), the *Aster albescens* group (described in this series as the genus *Sinosidus*), and others.

Aster longipetiolatus was transferred by Nesom (1993) with other Asian species into the otherwise American genus *Doellingeria*, but molecular data indicate that *Doellingeria* is strictly North American and that *A. longipetiolatus* is not closely related to the Asian species once included there. Instead, the species morphologically closest to *A. longipetiolatus* (Hengduan Mountains of Sichuan and Yunnan, China) are primarily Himalayan in distribution (Pakistan and Kashmir to Tibet, Nepal, and Indian states) and, as hypothesized here following earlier observations of Grierson (1964), constitute a monophyletic group. As part of the broader attempt to more clearly define *Aster* L. (e.g., Nesom 2020a, 2020b), these five species are recognized here as a separate genus.

CORDIOFONTIS Nesom, **gen. nov.** **TYPE**: *Cordiofontis peduncularis* (Wall. ex Nees) Nesom

Distinct in its rhizomatous-perennial, herbaceous habit, eglandular vestiture, stems often zig-zag at the nodes, leaves mostly cordate-petiolate, blades of proximal with basally dilated-sheathing petioles, heads solitary or few on few-bracteate peduncles in a loose corymb, outer phyllaries completely herbaceous, and fusiform, strigose, eglandular achenes with a biseriate pappus of acute-tipped bristles.

Perennial herbs from a short, thick, fibrous-rooted rhizome, colonizing by longer, slender rhizomes (the latter not commonly included in herbarium collections). **Stems** erect, often zig-zag at nodes, 15–l00 cm tall, glabrous to sparsely villous proximally, becoming long-villous on inflorescence branches, eglandular. **Leaves** cauline, largest at midstem, blades cordate or ovate to broadly lanceolate or elliptic-lanceolate, often discolorous (paler abaxially), glabrous to hirsute or hirsute-villous, eglandular, margins serrate to serrate-dentate, often coarsely so, venation camptodromous and prominently reticulate, petioles long and narrow, those of at least the proximal leaves dilated-winged

and sheathing at the base. **Heads** solitary or few in a loose corymb, on few-bracteate peduncles. **Involucres** shallowly campanulate to cupulate; phyllaries in 2–3 subequal series, lanceolate, outer green-herbaceous, inner stramineous with hyaline margins or sometimes with an herbaceous apical patch; receptacles epaleate. **Ray flowers** 18–45, ligules 12–25 mm long, purple to bluish. **Disc flowers** bisexual, fertile, corollas 3.5–7 mm long. **Achenes** obovate, 3–4.5 mm long, weakly compressed with 2 marginal veins, strigose, eglandular; pappus biseriate, inner series of barbellate, acute-tipped bristles about as long as the disc corollas (half as long in *C. flexuosa*), outer of bristles or bristle-like scales 0.3–1 mm long (in *C. longipetiolata*, pappus of only the short, outer series).

A chromosome number of $n = 27$ has been reported for *Cordiofontis peduncularis* (Gupta & Gill 1988, 1989; Gupta et al. 1989); $n = 9$ has been reported for *C. flexuosa* (Gupta & Garg 1987; Gupta et al. 1989; Jee et al. 1987).

Key to the species of *Cordiofontis*

1. Leaves sessile to short-petiolate; pappus bristles half as long as the disc corolla ..... **Cordiofontis flexuosa**
1. Leaves long-petiolate; pappus extremely short or bristles as long as the disc corolla.
    2. Pappus a series of scale-like bristles less than 1 mm long; Sichuan and Yunnan, China ..... **Cordiofontis longipetiolata**
    2. Pappus of barbellate bristles as long as the disc corollas; Himalayan region from Pakistan and Kashmir to Tibet, Nepal, and Indian states.
        3. Stems 15–20 cm high; phyllaries in 3 series ..... **Cordiofontis laka**
        3. Stems 10–90 cm high; phyllaries in 2 series.
            4. Stems mostly 30–90 cm high; leaf blades cuneate to rounded or truncate at base; phyllaries equalling or slightly longer than the disc corolla length ..... **Cordiofontis peduncularis**
            4. Stems mostly 10–15 cm high; leaf blades subcordate at base; phyllaries about twice as long as the disc corollas ..... **Cordiofontis nepalensis**

1. **Cordiofontis peduncularis** (Wall. ex Nees) Nesom, **comb. nov.** *Aster peduncularis* Wall. ex Nees, Gen. Sp. Ast., 24. 1832. **TYPE**: **INDIA**. **Uttarakhand**. Aster peduncularis Wallich 2967/77, Kamoon RB, *N. Wallich* (holotype: K-Wallich, Fig. 1; isotype: G-DC).

    Amphirhapis peduncularis DC., Prodr. 5: 344. 1836. **TYPE**: **INDIA**. **Uttarakhand**. Aster peduncularis Wallich 2967/77, Kamoon RB, *N. Wallich* (holotype: G-DC; isotypes: BM, E, K-2 (ex herb. Benthamianum & ex herb. Hookerianum), K-W). Types are cited here following Hind (2008).

    Himalayas from Pakistan and Kashmir to Himachal Pradesh, Uttarakhand, and Nepal. Figures 1, 2, 3, 14. Hind (2008) provided a history of the name, a detailed morphological description, a line drawing with details, and notes on garden cultivation.

2. **Cordiofontis nepalensis** (Grierson) Nesom, **comb. et stat. nov.** *Aster peduncularis* subsp. *nepalensis* Grierson, Notes Roy. Bot. Gard. Edinb. 26: 95. 1964. **TYPE**: **NEPAL**. Between Jumla and Garjigoth, 10,000 ft, 8 Aug 1952, *O. Polunin*, *W.R. Sykes,* & *L.H.J. Williams 5016* (holotype: E, Fig. 4; isotype: BM, Fig. 5).

    Nepal endemic. Figures 4, 5, 6.

3. **Cordiofontis flexuosa** (Royle ex Lindl.) Nesom, **comb. nov.** *Calimeris flexuosa* Royle ex Lindl. in DC., Prodr. 5: 258. 1836. *Aster thomsonii* C.B. Clarke, Comp. Ind., 48. 1876 [nom. nov., not *Aster flexuosus* Nuttall 1818]. **TYPE**: **INDIA**. **Kashmir**. Cachemire, 1833, *M. Royle 113*

(holotype: G-DC, Fig. 11). Protologue: "In Indiae orient. prov. Mussonee legit cl. Royle pl. exs. n. 113." Citation of the authority for *Calimeris flexuosa* follows that suggested by IPNI.

Diplopappus asperulus DC., Prodr. 5: 277. 1836. *Aster asperulus* (DC.) Hook. f., Fl. British India 3: 252. 1881 (not *Aster asperulus* Wall. ex Nees 1832, nom. nud.; not *Aster asperulus* Torrey & Gray 1841). **TYPE**: **INDIA**. **Uttarakhand**. Aster asperulus Wallich 2968/78, Kamoon, *N. Wallich* (holotype: G-DC G00494320; isotypes: BM, K-Wallich, Fig. 13).

Pakistan, India (Kashmir, Himachal Pradesh, Uttarakhand, Uttar Pradesh,). Figures 11, 12, 13, 14, 15. A detailed and technical description of this species is provided in Kletter and Kriechbaum (2001).

Cordiofontis flexuosa (as *Aster thomsonii*) was said to be one of the parents of the garden hybrid *Aster* × *frikartii* Silva Tar. & C.K. Schneid. (Freiland-Staud., ed. 4. 1927), created by the Swiss gardener Carl Ludwig Frikart in 1918. The other was said to be *Aster amellus* L., the type species of *Aster* L. In all, Frikart created four different cultivars from this cross, which now appear even more remarkable as they are intergeneric hybrids. Other examples of intergeneric hybrids in Astereae are given by Nesom (1994).

4. **Cordiofontis laka** (C.B. Clarke) Nesom, **comb. nov.** *Aster laka* C.B. Clarke, Comp. Ind., 49. 1876. **TYPE**: "Western Himalaya, Laka, near Dhurmsala, 10,000-11,000 ft, 17 Oct 1874, *C.B. Clarke 23869* (holotype: K, Fig. 10). Protologue: "Ad Laka prope Dhurmsala in Himalaya borealioccidentali ad 11000 ped. alt. mense Oct. florens."

   India (Kashmir, Himachal Pradesh).

5. **Cordiofontis longipetiolata** (C.C. Chang) Nesom, **comb. nov.** *Aster longipetiolatus* C.C. Chang, Sunyatsenia 6: 22. 1941. *Kalimeris longipetiolata* (C.C. Chang) Y. Ling, Fl. Reipubl. Popularis Sin. 74: 108. 1985. *Doellingeria longipetiolata* (C.C. Chang) Nesom, Phytologia 75: 457. 1993 [1994]. **TYPE**: **CHINA**. **Sichuan**. [label has "Precise locality not known"], 30 Jun 1936, *K.L. Chu 3023* (holotype: PE image, Fig. 9; isotypes: P-Fig. 8, SYS, W-Fig. 7). Protologue: "Pao-Hsing-Hsien, Mai-Li-Chuan, Ning-Chang-Kao, 2500 m, along the stream."

   Aster trichanthus Hand.-Mazz., Oesterr. Bot. Zeit. 90: 125. 1941. **TYPE**: **CHINA**. **Sichuan**. Paohsing-hsien, 30 Jun 1936, *K.L. Chu 3023* (holotype: W, Fig. 7; isotypes: P-Fig. 8, PE, Fig. 9, SYS). Protologue: "W.-Setschwan: Paohsing (Mupin)."

   China (Sichuan, Yunnan).

   This species is set apart geographically from the others and dilated-sheathing petiole bases are seen only on the basalmost leaves — it may not belong here, in which case it would be justifiably recognized as a monotypic genus, based on its isolated evolutionary position according to the molecular data.

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Figure 1. *Cordiofontis peduncularis*. Holotype of *Aster peduncularis* Wall. ex Nees (Wallich 2967/77, K-Wallich).

Figure 2. *Cordiofontis peduncularis*. Representative collection, Uttarakhand (E).

Figure 3. *Cordiofontis peduncularis*. Representative collection, Himachal Pradesch (E).

Figure 4. *Cordiofontis nepalensis*. Holotype (E).

Figure 5. *Cordiofontis nepalensis*. Isotype (BM).

Figure 6. *Cordiofontis nepalensis*. Representative collection, *Polunin et al. 5436* (E).

Figure 7. *Cordiofontis longipetiolata*. *Chang 3023* (W). Holotype of *Aster trichanthus* and isotype of *Aster longipetiolatus*.

Figure 8. *Cordiofontis longipetiolata*. *Chang 3023* (P). Isotype of *Aster trichanthus* and isotype of *Aster longipetiolatus*. Basal leaves have petioles with a dilated, clasping base.

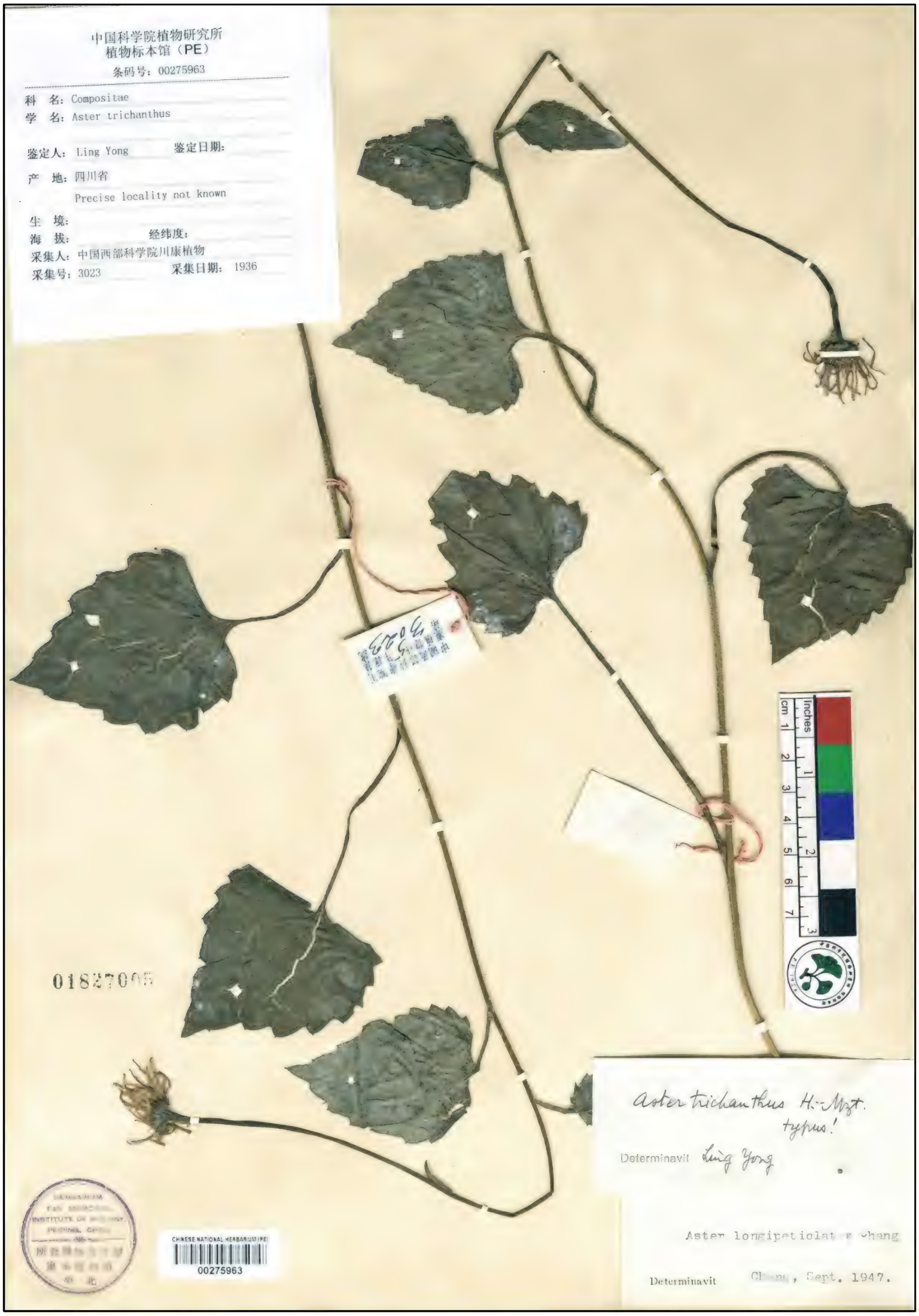

Figure 9. *Cordiofontis longipetiolata*. *Chang 3023* (PE). Holotype of *Aster longipetiolatus* and isotype of *Aster trichanthus*.

Figure 10. *Cordiofontis laka*. Holotype of *Aster laka* (K).

Figure 11. *Cordiofontis flexuosa*. Holotype, *Calimeris flexuosa* Royle ex Lindl. in DC. (G-DC).

Figure 12. *Cordiofontis flexuosa*. Representative collection, Simlen, Himalaya, *Thomson s.n.* (BM).

Figure 13. *Cordiofontis flexuosa*. Isotype of *Diplopappus asperulus* DC. (Aster asperulus of Wallich, 2968/78, K-W).

Figure 14. *Cordiofontis flexuosa*. Representative collection (E).

Figure 15. *Cordiofontis peduncularis*. Beth Chatto's Plants & Gardens (website).

Figure 16. *Cordiofontis flexuosa*. Lidderwat in Jammu & Kashnmir. Photo by J.D.A. Stainton (Royal Botanic Garden Edinburgh).

Nesom, G.L. 2020. *Cardiagyris* (Asteraceae: Astereae), a new genus for the *Doelllingeria*-like species of Asia. Phytoneuron 2020-61: 1–26. Published 3 August 2020. ISSN 2153 733X

CARDIAGYRIS (ASTERACEAE: ASTEREAE), A NEW GENUS FOR THE *DOELLLINGERIA*-LIKE SPECIES OF ASIA

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ABSTRACT

Nine species of Asian *Aster* and one hybrid are placed in **Cardiagyris** Nesom, **gen. nov.**, typified by *Aster scaber* Thunb.: ***Cardiagyris dimorphophylla*** (Franch. & Sav.) Nesom, **comb. nov.**, ***Cardiagyris dolichophylla*** (Y. Ling) Nesom, **comb. nov.**, ***Cardiagyris huangpingensis*** (W.P. Li & Z. Li) Nesom, **comb. nov.**, ***Cardiagyris japonica*** (Miq.) Nesom, **comb. nov.**, ***Cardiagyris komonoensis*** (Makino) Nesom, **comb. nov.**, ***Cardiagyris marchandii*** (Levl.) Nesom, **comb. nov.**, ***Cardiagyris rugulosa*** (Maxim.) Nesom, **comb. nov.**, ***Cardiagyris scabra*** (Thunb.) Nesom, **comb. nov.**, ***Cardiagyris sohayakiensis*** (Koidzumi) Nesom, **comb. nov.**, and the hybrid ***Cardiagyris*** × ***sekimotoi*** (Makino) Nesom, **comb. nov.** Phylogenetic analyses based on molecular data place the *Cardiagyris* species at the base of the *Asterothamnus* branch of subtribe Asterinae, which includes other genera treated as separate from *Aster* sensu stricto. All species except *C. marchandii* have been included in molecular analyses, but a well-supported phylogeny is lacking. Morphological coherence of the genus is strong. Tentative evidence suggests that narrowly lanceolate leaves have evolved independently from cordate-petiole ones, once in China and once in Japan.

Aster scaber Thunb. and its close relatives have long been recognized as a distinctive natural group and the recent description of two species from southern China (Guangxi and Guizhou) have recalled attention to it. *Aster scaber* and *A. marchandii* Levl. were transferred to the American genus *Doellingeria* (by C.G.D. Nees in 1832, Y. Ling in 1975), and Nesom (1993) placed the remaining Asian species there. The similarities, however, are evolutionarily convergent, as molecular sequence data unequivocally show that the American species arose within a North American lineage (e.g., Noyes & Rieseberg 1999) while the Asian species are part of a lineage of Old World taxa (Ito et al. 1998; W.-P. Li et al. 2012; Z. Li et al. 2020; summary in Nesom 2020a).

The closest relatives (fide molecular analyses) to the doellingerioid Asian species include newly described genera *Yonglingia*, *Changchaochienia*, and *Sinobouffordia* (Nesom 2020b) as well as the more generally accepted accepted genera *Arctogeron* DC. and *Asterothamnus* Novop. *Cardiagyris* species are distinct in karyotype from other Asian species (reviewed by Saito et al. 2007).

CARDIAGYRIS Nesom, **gen. nov.** **TYPE**: *Cardiagyris scabra* (Thunb.) Nesom

Kalimeris sect. *Cordifolium* Kitam., Mem. Coll. Sci. Kyoto Univ., ser. B. 8: 312. 1937. *Doellingeria* sect. *Cordifolium* (Kitam.) Nesom, Phytologia 75: 456. 1993. *Doellingeria* ser. *Cordifolium* (Kitam.) Nesom, Phytologia 75: 456. 1993. **LECTOTYPE** (Nesom 1993): *Biotia japonica* Miq.

Doellingeria [sect. *Cordifolium*] ser. *Papposae* Nesom, Phytologia 75: 457. 1993. **TYPE**: *Doellingeria scabra* (Thunb.) Nesom

Aster sect. *Teretachaenium* Kitam., Mem. Coll. Sci. Kyoto Univ., ser. B, 8: 3357. 1937. **LECTOTYPE** (Nesom 1993): *Aster scaber* Thunb.

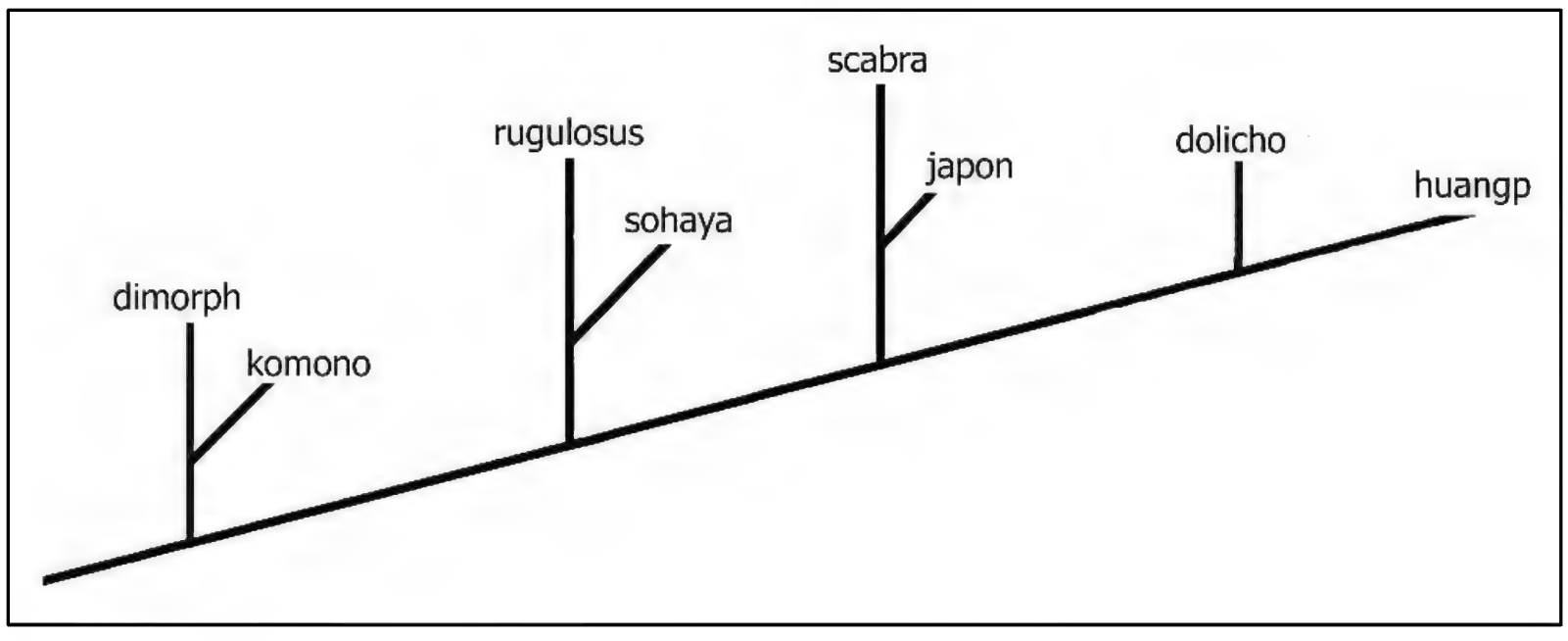
Aster ser. *Sohayakienses* Kitam., J. Jap. Bot. 12 722. 1936. **TYPE**: *Aster sohayakiensis* Koidz.

Distinct in its combination of herbaceous perennial habit from rhizomes, eglandular vestiture, either cordate- or ovate-petiolate or lanceolate-sessile to lanceolate-petiolate leaves, shallow involucres, thick-herbaceous phyllaries, heads on ebracteate peduncles in a loose corymb, rays few and white, achenes obovoid-cylindric and subterete, multinerved, elongating to equal or greater than the involucre height, and pappus of clavate-tipped bristles.

Perennial herbs from a compact, fibrous-rooted caudex, sometimes with short rhizomes or stolons. **Leaves** basal (usually withered by anthesis) and cauline, lanceolate-sessile to lanceolate-petiolate or cordate-petiolate to ovate-petiolate, glabrous, sometimes glaucous abaxially, margins serrate to crenate or dentate or subentire, venation weakly brochidodromous, basal actinodromous, or camptodromous. **Heads** in a loose corymb or panicle, rarely solitary, peduncles ebracteate or with 1 small bract (more in *C. dolichophyllus* and *C. huangpingensis*). **Involucres** campanulate to broadly campanulate; phyllaries broadly elliptic to elliptic-oblong or narrowly triangular, evenly thickened (thin-herbaceous in *C. dolichophylla*), (2–)3–4-seriate, unequal to subequal, not keeled, margin scarious; receptacles epaleate. **Ray flowers** 4–20 in 1 series, ligules white, sometimes gradually becoming pink. **Disk flowers** fertile, lobes narrowly triangular, reflexing-coiling. **Achenes** obovoid-cylindric, very slightly compressed, variably 3-7-ribbed, 3–5 mm long, glabrous to sparsely short-strigose; pappus of barbellate bristles in 3–4 series of uneven length, innermost about as long as the disc corollas, clavate-tipped, outermost much shorter, or in *C. japonica* and *C. marchandii* all pappus elements much shorter than the disc corollas. 2n = 18.

An apparent dichotomy in leaf morphology exists among the *Cardiagyris* species. Leaves of five species, including *Cardiagyris scabra* (the type, widespread) and four others (either Japan or China) have ovate to ovate-deltate blades with abruptly delimited petioles. Leaves of *C. rugulosa* – *C. soyahakiensis* (Japan) and *C. dolichophylla* – *C. huangpingensis* (China) have mostly narrowly lanceolate to elliptic-lanceolate blades long-attenuate to a gradually delimited petiolar portion. It is probable that *C. rugulosa*/*soyahakiensis* and *C. dolichophylla*/*huangpingensis* are paired evolutionarily as well as geographically, but preliminary evidence does not indicate that these pairs are most closely related to each other. As noted below, *C. scabra* (ovate leaves) and *C. rugulosa* (lanceolate leaves) are sympatric in Japan and occasionally hybridize to produce morphological intermediates. *Cardiagyris scabra* and *C. marchandii* (ovate) are sympatric in China with *C. dolichophylla* and *C. huangpingensis* (lanceolate), but there apparently is no overlap in ecology and hybrids have not been noted.

Cladograms have been published for phylogenetic studies with more than one species of *Cardiagyris* (Ito et al. 1994, 1998; Brouillet et al. 2009; Soejima & Hamashima 2019; Z. Li et al. 2020), but species included and molecular underpinning have varied. The diagram below attempts, intuitively, to summarize hypotheses of putative relationships but it should be interpreted only as speculative. *Cardiagyris marchandii* has not been included in molecular sampling.



A. LEAF BLADES OVATE, PETIOLES ABRUPTLY DELIMITED

1. **Cardiagyris scabra** (Thunb.) Nesom, **comb. nov.** *Aster scaber* Thunb., Fl. Jap., 316. 1784. *Doellingeria scabra* (Thunb.) Nees, Gen. Sp. Aster., 183. 1832. *Eucephalus scaber* (Thunb.) Gandoger, Bull. Soc. Bot. France 65: 40. 1918. **TYPE**: **JAPAN**. [No other collection data], *C.P. Thunberg s.n.* (holotype: S image).

Biotia discolor Maxim., Prim. Fl. Amur., 146. 1859. *Biotia corymbosa* var. *discolor* (Maxim.) Regel, Tent. Fl. Uss. 33. 1864. **TYPE MATERIAL**: **CHINA**. Manchuria, Amur, no date, *Maximowicz s.n.* (P 711746 [ex LE] image; P 711747 [gift from LE] image). Manchuria, Amur, 29 Aug 1855, *R. Maack s.n.* (GH 283649 [with LE label] image; GH 283650 [no label] image).

Aster komarovii H. Léveillé, Bull. Acad. Int. Géogr. Bot. 20(1): 142. 1909. **TYPE**: **SOUTH KOREA**. Jeju Island ["In silvis Quelpaert"], Oct 1906, *U.J. Faurie 1125* (holotype: E).

Eastern China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hebei, Heilongjiang, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Nei Mongol, Shaanxi, Shandong, Shanxi, Sichuan, Zhejiang), Japan, Korea, Manchurian region of Russia. Figures 1-4.

2. **Cardiagyris marchandii** (Levl.) Nesom, **comb. nov.** *Aster marchandii* Levl., Fedde Repert. Sp. Nov. 11: 306. 1912. *Doellingeria marchandii* (Levl.) Ling, Icon., Cormorph. Sin. 4: 423. 1975. **TYPE**: **CHINA**. [**Guizhou**]. Kouy-Tchéou, Col de Hong Kouan La sou, 28 Aug 1911, *J. Esquirol 2736* (holotype: E image; isotype: K image).

Southeastern China (Fujian, Guangdong, Guangxi, Guizhou, Hubei, Jiangxi, Sichuan, Zhejiang). Figure 5.

3. **Cardiagyris japonica** (Miq.) Nesom, **comb. nov.** *Biotia japonica* Miq., Ann., Mus. Bot. Lugduno-Batavum 2: 170. 1866. *Aster japonicus* (Miq.) Franch. & Sav., Enum. Pl. Japon. 2: 398. 1876 (not *Aster japonicus* Less. ex Nees 1832). *Aster miquelianus* Hara [nom. nov.], J. Jap. Bot. 12: 338. 1936. *Kalimeris miqueliana* (Hara) Kitam., Fl. Reipubl. Pop. Sin. 74: 108. 1985. *Doellingeria japonica* (Miq.) Nesom, Phytologia 75: 456. 1993. **TYPE**: **JAPAN**. Protologue: "In monte Fire Jama prope oppidum Karotsa ins. Kiusiu: PIEROT; aliis locis SIEBOLD et BUERGER legerunt. — Kon Gik iap."

Japan. Figures 6 and 10. *Cardiagyris japonica* is similar in overall appearance to *C. dimorphophylla*; the short pappus of the former led to its placement in *Kalimeris*.

1. Pappus 4 mm long ..... **Cardiagyris dimorphophylla**
1. Pappus 0.5–1.5 mm long ..... **Cardiagyris japonica**

4. **Cardiagyris dimorphophylla** (Franch. & Sav.) Nesom, **comb. nov.** *Aster dimorphophyllus* Franch. & Sav., Enum. Pl. Japon. 1: 224. 1875. *Doellingeria dimorphophylla* (Franch. & Sav.) Nesom, Phytologia 75: 457. 1993. **LECTOTYPE** (designated here): **JAPAN**. Hakone, in rupibus regionis montanae, 1866-74, *P.A.L. Savatier 602* (P 71659 image; isolectotype: P 711660 image). Protologue: "Hab. in rupestribus regionibus montanae: in jugo Hakone (Savatier, n. 602). Fl. Aug. Sept." The protologue also cites a collection by Tanaka (P-2 sheets images).

Japan. Triploid clones occur at low frequencies among diploids in Kanagawa Prefecture (Matsuda & Shibata 1978). Figures 7-9, 10.

5. **Cardiagyris komonoensis** (Makino) Nesom, **comb. nov.** *Aster komonoensis* Makino, Tokyo Bot. Mag. 12: 65. 1898. *Doellingeria komonoensis* (Makino) Nesom, Phytologia 75: 457. 1993. **TYPE**: **JAPAN**. Prov. Ise: Mt. Komono-yama, Aug 1889, *M. Miyoshi s.n.* (herb. Sc. Coll. Imp. Univ. Tokyo, not seen). Makino noted that "Prof. M. Miyoshi once figured and described in

this Magazine as above quoted, but with no scientific name." Bot. Magaz., Tokyo, II. p. 71, tab. V. 1888 (reproduced in Fig. 11).

Japan. Figures 11-13.

B. LEAF BLADES NARROWLY LANCEOLATE, PETIOLES GRADUALLY DELIMITED

6. **Cardiagyris rugulosa** (Maxim.) Nesom, **comb. nov.** *Aster rugulosus* Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg 15: 226. 1871. *Doellingeria rugulosa* (Maxim.) Nesom, Phytologia 75: 456. 1993. **TYPE**: **JAPAN**. Yokahama, 1862, *C.J. Maximowicz 14501* (holotype: LE presumably, not seen; isotypes: GH, K, M, MO, NY, P-3 sheets, US; images of all). Only the MO sheet, with a handwritten label, has the number 14501.

Aster rugulosus var. *shibukawaensis* Kitam. & Murata, Acta Phytotax. Geobot. 19: 69. 1962. **TYPE**: **JAPAN**. Honshu, Prov. Totomi, Shibukawa, Inasatyo, Inasagun, 23 Sep 1959, *G. Murata 13105* (holotype: KYO, not seen but presumably the plant shown in Fig. 8 (photo) of the protologue).

Murata (1962) noted in the protologue that var. *shibukawaensis* is distinguished by hirsute and more branched stolons, more robust stems, and shorter and sometimes bracteate peduncles. Descriptions and photos of var. *shibukawaensis* are posted here: <http://mikawanoyasou.org/ data/sibukawasirogiku.htm> and <https://www.botanic.jp/plants-sa/ sibuka.htm>. The variety is included in lists of threatened Japanese plants but it is not clear that its taxonomy has been critically examined. It was not treated in the account by Ito and Soejima (1995), even in synonymy.

Japan. Figures 14, 15.

Cardiagyris × **sekimotoi** (Makino) Nesom, **comb. nov.** *Aster sekimotoi* Makino, J. Japanese Bot. 7: 10. 1931. *Doellingeria sekimotoi* (Makino) Nesom, Phytologia 75: 457. 1993. **TYPE**: **JAPAN**. Prov. Shimotsuke, Mt. Kasakake, *H. Sekimoto s.n.* (holotype: KYO, not seen). The description has this: "Leaves elliptical-ovate to broadly lanceolate, … cuneate towards the base," but Makino noted that "This species is very closely allied to *A. scaber* Thunb., having the non-cordate and depressed-dentate leaves."

Aster × *hashimotoi* Kitamura, Acta Phytotax. Geobot. 3: 130. 1934. **TYPE**: **JAPAN**. Prov. Ohmi, Hondo, Gamogun, Ichinebemura, Fuseno-tame, 10 Sep 1933, *Ch. Hashimoto s.n.* (holotype: KYO, not seen). Described by Kitamura as a hybrid, *Aster scaber* × *Aster rugulosus*.

Cardiagyris × *sekimotoi* is morphologically intermediate between *C. scabra* and *C. rugulosa*. Saito et al. (2007) showed that hybrids have low pollen fertility and exhibit additivity in ITS sequences, possessing nucleotide polymorphisms at 22 substitution sites, at positions where parents differ. Parents and hybrids are diploid. The hybrids occur at low frequency, hybrid swarms are absent, and they are "likely the result of repeated, reciprocal hybridizations."

7. **Cardiagyris sohayakiensis** (Koidz.) Nesom, **comb. nov.** *Aster sohayakiensis* Koidz., Tokyo Bot. Mag. 37: 56. 1923. *Doellingeria sohayakiensis* (Koidz.) Nesom, Phytologia 75: 456. 1993. **Type**: **JAPAN**. Wakayama (Kii), Doro-Hattcho, 29 Jul 1922, *G. Koidzumi s.n.* (KYO, not seen).

Aster ohtanus Makino, J. Jap. Bot. 3: 18. 1926. **TYPE**: **JAPAN**. The protologue cited three collections from the same locality: Prov. Kii: Doro-hatchô, on rocks, Oct 1922 and Sep 1924", *U. Ôta s.n.* and 8-9 Sep 1924, *T. Makino s.n.* (not seen, photo of inflorescence in the protologue).

Japan, narrowly endemic to the Wakayama and Nara prefectures (Kii Peninsula). Figure 16. Makino noted in the protologue that "This species is closely allied to *Aster rugulosus* Maxim., and yet they grow at quite different localities." Distinctions in the couplet below are from Ito and Soejima (1995).

1. Peduncle 5–10 cm long, ebracteate; disc corollas 6–8 mm long ..... **Cardiagyris rugulosa**
1. Peduncle 2–4 cm long, bracteate; disc corollas 4–5 mm long ..... **Cardiagyris sohayakiensis**

8. **Cardiagyris dolichophylla** (Y. Ling) Nesom, **comb. nov.** *Aster dolichophyllus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 357. 1985. **TYPE**: **CHINA**. **Guangxi**. Longshenging Shan Village (25° 48'05" N, 110° 00'15" E), 830 m, 14 Oct 1955, *Guangfu Forest District Collecting Team 1056* (IBK image).

Guangxi, narrowly endemic. Illustrations: Fig. 516 in Flora of China (Chen et al. 2011); Fig. 6 in Zhang et al. (2019); Fig. 6 in Z. Li et al. (2020). Specimen images through Chinese Virtual Herbaria (website: National Plant Specimen Resource Center). Figures 18-20.

9. **Cardiagyris huangpingensis** (W.P. Li & Z. Li) Nesom, **comb. nov.** *Aster huangpingensis* W.P. Li & Z. Li, Phytotaxa 433: 242. 2020. **TYPE**: **CHINA**. **Guizhou**. Qiandongnan Miao and Dong Autonomous Prefecture, Huangping County, Grand Feiyun Canyon, 26° 55'06" N, 108° 01'53.10" E, riverbanks in a valley, 650 m, 13 Sep 2017, *LWP-LZ1709-015* (holotype HNNU, Fig. 17; isotypes: *LWP-LZ1709-006*, *LWP-LZ1709-007*, and *LWP-LZ1709-008*, all HNNU).

Guizhou, apparently known only from the type locality. Rocky stream banks at 650–680 meters. Illustrations: Fig. 5 in Z. Li et al. (2020). Figure 17.

1. Blades of proximal leaves lanceolate with acute to acuminate apex, 10–17 cm long, similar distally; phyllaries thin-herbaceous, loose and spreading, middle with ciliate-eglandular margins; disc flowers (26–)30–44, collecting appendages oblong-triangular ..... **Cardiagyris dolichophylla**

1. Blades of proximal leaves obovate with rounded to obtuse apex, 3–7.5 cm long, becoming narrowly oblanceolate to lanceolate distally; phyllaries thickened, rigid and tightly appressed, middle with glandular margins; disc flowers 16–28, collecting appendages triangular-deltate ..... **Cardiagyris huangpingensis**

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Figure 1. *Cardiagyris scabra*. Siberia. *Shvedchikova s.n.* (MW).

Figure 2. *Cardiagyris scabra*. Siberia. *Dudov 2016_S_041* (MW).

Figure 3. *Cardiagyris scabra*. Japan. Photo by Masashi Igari, Plants Index Japan.

Figure 4. *Cardiagyris scabra*. Top: Japan, photographer unknown. Bottom: Manchuria, Amur, detail from type material of *Biotia discolor*, *Maack s.n.* (GH).

Figure 5. *Cardiagyris marchandii*. China (Guangxi). *K.J. Yan 451029130912015* (GXMG).

Figure 6. *Cardiagyris japonica*. Japan. *Murata 18654* (US).

Figure 7. *Cardiagyris dimorphophylla*. Japan. Collector not specified, s.n. (US). This plant is close in morphology to the type.

Figure 8. *Cardiagyris dimorphophylla*. Japan. *Asai 7411* (US).

Figure 9. *Cardiagyris dimorphophylla*. Japan. Collector not specified, s.n. (US).

Figure 10. Involucres and flowers. Top: *Cardiagyris japonica*. Bottom: *Cardiagyris dimorphophylla*.

Figure 11. *Cardiagyris komonoensis*. Tokyo Bot. Mag. 2(15): 71, tab. 5. 1888.

Figure 12. *Cardiagyris komonoensis*. Japan. *Saito 5533* (US).

Figure 13. *Aster komonoensis*. Mount Gozaisho, Komono, Mie Prefecture, Japan. Wikipedia.

Figure 14. *Cardiagyris rugulosa*. Japan. *Furuse 13044* (PE).

Figure 15. *Cardiagyris rugulosa*. Japan. *Furuse 51333* (PE).

Figure 16. *Cardiagyris sohayakiensis*. Japan. *Furuse 39493* (PE).

Figure 17. *Cardiagyris huangpingensis*. Holotype (HNNU), from Li et al. (2020).

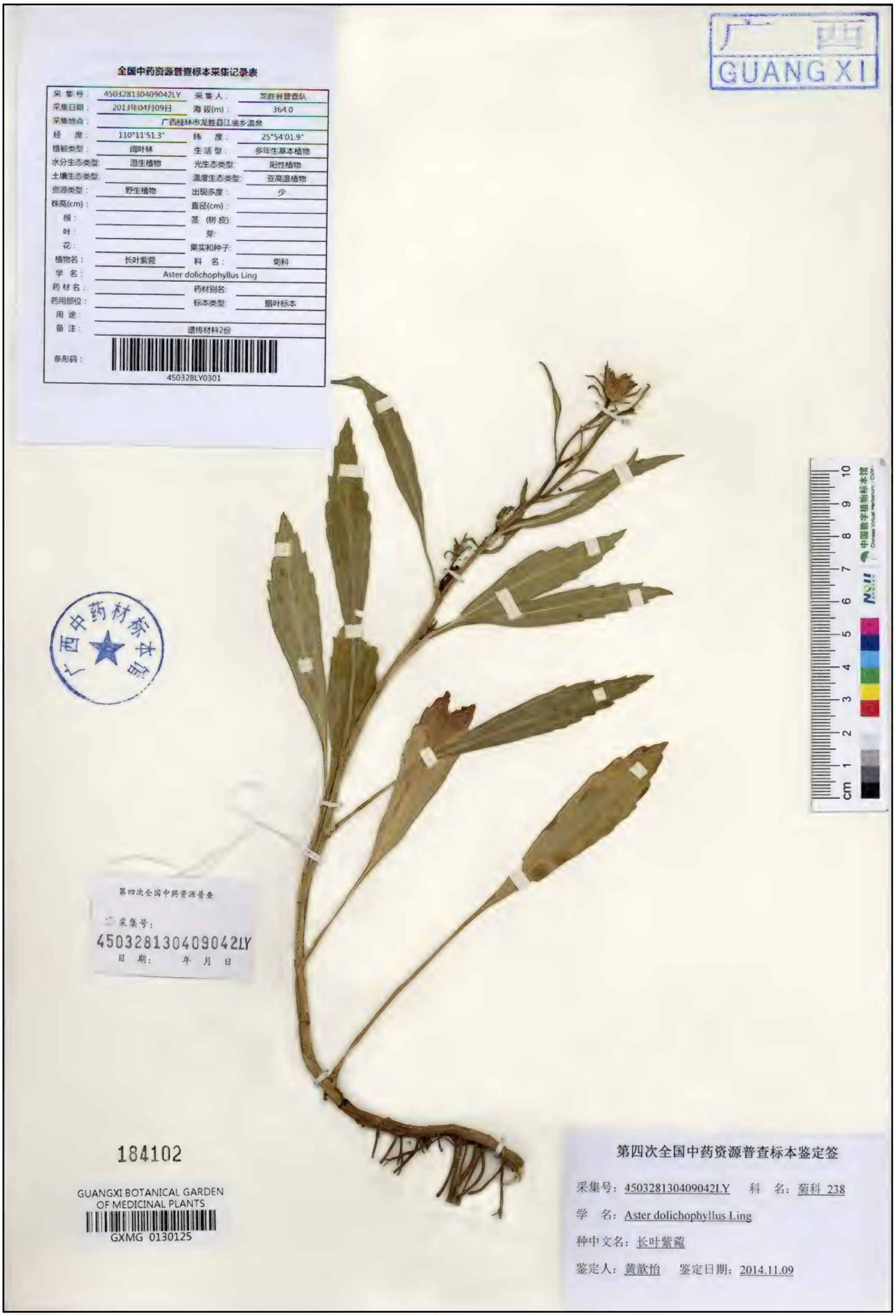

Figure 18. *Cardiagyris dolichophylla*. Guangxi. *Longsheng County Census Team* (GXMG).

Figure 19. *Cardiagyris dolichophylla*. Guangxi. *Chen & Jiang EM271* (KUN).

Figure 20. *Cardiagyris dolichophylla*. PlantTong ZhiWuTong.com <https://www.zhiwutong.com/latin/Compositae/Aster-dolichophyllus-Ling.htm> The spreading, herbaceous, lanceolate phyllaries with sharply acute apices are unique among the species of *Cardiagyris*. See images contrasting involucral morphology of *C. dolichophylla* and *C. huangpingensis* in Z. Li et al. (2020, Fig. 6E).

Nesom, G.L. 2020. Lectotypification of *Heterochaeta* DC. (Asteraceae). Phytoneuron 2020-62: 1. Published 17 August 2020. ISSN 2153 733X

LECTOTYPIFICATION OF *HETEROCHAETA* DC. (ASTERACEAE)

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ABSTRACT

Heterochaeta DC. (1836) is lectotypified by *Heterochaeta erigeroides* DC. (= *Erigeron uniflorus* L.) and the name becomes a synonym of *Erigeron* L.

The genus *Heterochaeta* was established by A.P. de Candolle to include six species, each now recognized as a member of Asteraceae tribe Astereae.

Heterochaeta diplostephioides DC., Prodr. 5: 282. 1836. = **Aster diplostephioides** (DC.) Benth. ex C.B. Clarke
Heterochaeta hispida DC., Prodr. 5: 282. 1836. = **Hysterionica jasionoides** Willd.
Heterochaeta erigeroides DC., Prodr. 5: 282. 1836. = **Erigeron uniflorus** L.
Heterochaeta asteroides DC., Prodr. 5: 282. 1836. = **Aster asteroides** (DC.) Kuntze
Heterochaeta gnaphalioides (Kunth) DC., Prodr. 5: 282. 1836. = **Laennecia confusa** (Cronq.) Nesom
Heterochaeta pubescens (Kunth) DC., Prodr. 5: 283. 1836. = **Erigeron pubescens** Kunth

Three species were added to the genus by George Bentham and Alexander von Bunge. Neither made any comment regarding the definition of the genus, although Bunge explicitly compared his *Heterochaeta pseuderigeron* to de Candolle's *H. diplostephioides*, *H. erigeroides*, *H. asteroides*, and *H. hispida*.

Heterochaeta stricta Benth., Pl. Hartw. 206. 1845. = **Laennecia gnaphalioides** (Kunth) Cass.

Heterochaeta leucophylla Bunge, Mém. Acad. Imp. Sci. St.-Pétersbourg Divers Savans 7: 325. 1847. = **Psychrogeton amorphoglossus** (Boiss.) Novopokr.

Heterochaeta pseuderigeron Bunge [as "pseud-erigeron"], Beitr. Fl. Russl. 150. 1852. = **Psychrogeton pseuderigeron** (Bunge) Novopkr. ex Nevski

Heterochaeta might have been used as the name for a group of species segregated from Asian *Aster* (including *A. diplostephioides* and *A. asteroides*; Nesom 2020), but its reference to "diverse setae" (outer pappus series much shorter than the inner) is ambiguous, applying to various genera of Astereae, and the species of de Candolle's original genus are now recognized among four different genera. The few early additions to the genus further increased its heterogeneity and the name has not been subsequently used. The lectotype chosen here places *Heterochaeta* as a synonym of *Erigeron* L.

Heterochaeta A.P. de Candolle, Prodr. 5: 282. Oct (prim.) 1836 (non Besser 1827).
LECTOTYPE (designated here): *Heterochaeta erigeroides* DC. = *Erigeron uniflorus* L.

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TIBETIODES NESOM, GEN. NOV. (ASTERACEAE: ASTEREAE), INCLUDING 27 SPECIES OF HIMALAYAN *ASTER*

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ABSTRACT

Tibetiodes Nesom, **gen. nov.**, includes 27 species primarily Himalayan in geography — *T. flaccida* ranges significantly more broadly and several other species occur outside of the Tibetan plateau. Molecular sequence data indicate that 7 of these species are monophyletic and distantly related to Aster sensu stricto (in the sense of Li et al 2012). The addition here of other species is based on their morphological coherence in a set of features, particularly and consistently by ray florets in 2–3 series and with short tubes and elongate styles. The following constitute the genus, all as new combinations in *Tibetiodes*: ***T. angustior***, ***T. asteroides***, ***T. bietii***, ***T. brachytricha***, ***T. brevis***, ***T. bulleyana***, ***T. diplostephioides***, ***T. falconeri***, ***T. farreri***, ***T. flaccida***, ***T. glandulosa***, ***T. himalaica***, ***T. jeffreyana***, ***T. labrangensis***, ***T. latibracteata***, ***T. latisquamata***, ***T. likiangensis***, ***T. lipskii***, ***T. nepalensis***, ***T. retusa***, ***T. salwinensis***, ***T. setchuenensis***, ***T. stracheyi***, ***T. techinensis***, ***T. tientschwanensis***, ***T. tsarungensis***, and ***T. yunnanensis***. Formal nomenclature is provided for each species and synonyms. Lectotypes are designated for *A. brachytrichus*, *A. delavayi*, *A. diplostephioides* var. *falconeri*, *A. falconeri* var. *nepalensis*, *A. farreri*, *A. flaccidus* var. *fructu-glandulosus*, *A. himalaicus*, *A. labrangensis*, *A. latibracteatus*, *A. likiangensis*, *A. mekongensis*, *A. salwinensis*, *A. stracheyi*, *A. vilmorinii*, and *A. yunnanensis*.

Molecular sequence data indicate that a group of primarily Himalayan species of *Aster* L. is monophyletic and evolutionarily distinct from even the broad range of species considered by Li et al. (2012) to constitute the genus. Six of the species were initially studied by Li et al.; *Aster salwinensis* was added to the set by Zhang et al. (2015), who updated the cladistic topology as in Figure 1. Li et al. (2012) acknowledged that this group of species "might become a new genus" and that is the course taken here. The group is part of the Asterothamnus branch of subtribe Asterinae (Nesom 2020a, 2020b).

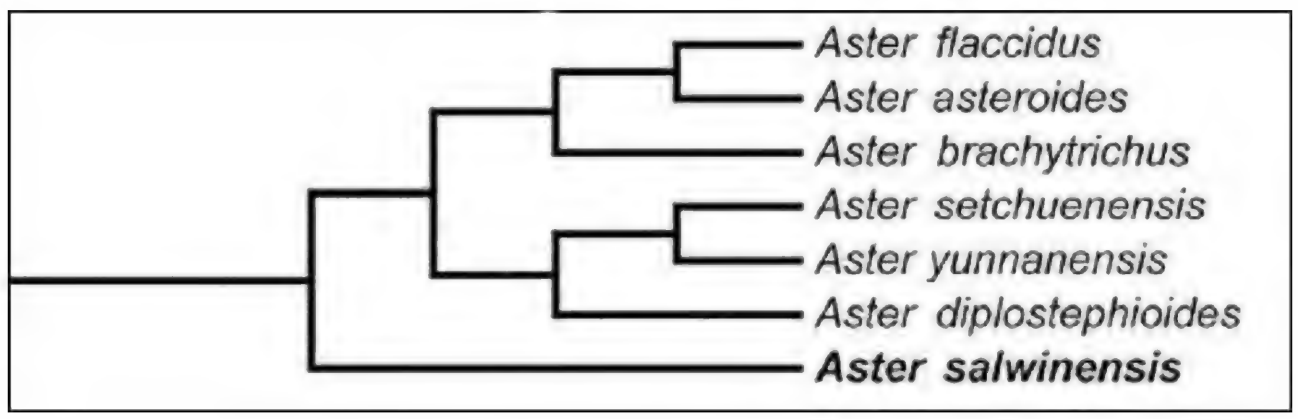

Figure 1. Relationships of seven species of *Aster* based on a combined data set (nuclear ribosomal DNA internal and external transcribed spacer sequences and plastid genome DNA trnL-F sequences). Modified from Zhang et al. (2015).

Grierson (1964) recognized the morphological coherence of these species, placing them in subsects. *Homochaeta* and *Heterochaeta* of *Aster* sect. *Alpigeni* in his classification. His observations add 6 species to those outlined above in Figure 1: *A. bietii*, *A. falconeri*, *A. himalaicus*, *A. latibracteatus*, *A. retusus*, and *A. stracheyi* (*A. tricephalus*, *A. neo-elegans*, and *A. barbellatus* of Grierson's subsect. *Heterochaeta* are not part of the group considered here). The survey here adds another 14 species.

TIBETIODES Nesom, **gen. nov.** **TYPE**: *Tibetiodes diplostephioides* (DC.) Nesom

See Nesom (2020c) for the taxonomic disposition of *Heterochaeta* DC., which might have been used as the name for this genus.

Perennial herbs from a short, thickened, fibrous-rooted rhizome (stolons in *T. stracheyi*); cauline leaves oblong to elliptic-lanceolate, ovate, or elliptic-obovate, entire or with a few, shallow teeth or mucros, epetiolate, often subclasping; heads mostly 1; phyllaries mostly evenly herbaceous, lanceolate-triangular to lanceolate-oblong, usually longer than the disc flowers; ray flowers in 2–3 series (sometimes 1), light blue-violet to violet, tube short and styles elongate, ligules narrow, coiling; disc corollas often darkening or becoming deep violet in age; achenes narrowly obovate to oblanceolate-obovate, strongly compressed, 2-nerved; pappus usually of 2 series, the inner of relatively few, thickened bristles, the outer of short scales (all of the pappus short in *T. brachytricha*).

Tibetiodes species mostly are restricted the Himalayan region (Tibetan Plateau). The ranges of *T. asteroides*, *T. diplostephioides*, and *T. labrangensis* extend to Gansu and Qinghai; *T. farreri* occurs only in central China, not reaching the Himalayas, and *T. lipskii* is restricted to Gansu and Qinghai.

Unambiguously diagnostic features of the genus are in the ray flowers, which are consistently violet and usually occur in 1 or (most commonly) 2–3 series, producing short tubes and prominently long styles. In situ photos (Figs. 2-9) show the long styles.

Most of the species have well-developed cauline leaves, but some have leaves mostly in a basal rosette, with cauline strongly reduced (*Tibetiodes asteroides*, *T. flaccida*, *T. glandulosa*, *T. jeffreyana*, *T. likiangensis*, *T. retusa*, *T. tientschwanensis*). Variation in habit and morphology in Figs. 13-26.

Phyllaries in a few species are narrow and thickenened (*Tibetiodes farreri*, *T. labrangensis*, *T. salwinensis*; e.g., Fig. 12), in contrast to the broad and evenly herbaceous phyllaries characteristic of most. Variation in phyllary morphology is shown in Figs. 10-12.

A morphological subgroup includes *Tibetiodes angustior*, *T. brevis*, *T. diplostephioides*, *T. labrangensis*, *T. lipskii*, and *T. yunnanensis* — these have persistent, fibrous petiole bases (e.g., Figs. 14, 17, 18). *Tibetiodes angustior* and *T. labrangensis* (Fig. 17) consistently produce 3–5 heads per stem; *T. yunnanensis* usually is monocephalous but sometimes has 2–3 heads.

1. Tibetiodes angustior (Hand.-Mazz.) Nesom, **comb. et stat. nov.** *Aster yunnanensis* var. *angustior* Hand.-Mazz., Notizbl. Bot. Gart. Berlin-Dahlem. 13: 622. 1937. **TYPE**: **CHINA**. **Yunnan**. NW Yunnan, Tung-shan in der Yangtze-Schleife, 3050- 3350 m, offene, steinige Matten, Sep, 1913, *G. Forrest 11267* (holotype: E image; isotypes: BM image, K-2 sheets images).

China (Sichuan, Yunnan).

2. Tibetiodes asteroides (DC.) Nesom, **comb. nov.** *Heterochaeta asteroides* DC., Prodr. 5: 282. 1836. *Aster asteroides* (DC.) Kuntze, Revis. Gen. Pl. 1: 315. 1891. **TYPE**: **KASHMIR**. Cachemire, 1833, *M. Royle 114* (holotype: G-DC image).

Aster heterochaeta Benth. ex C.B. Clarke, Comp. Ind., 44. 1876 (nom. illeg. superfl.). *Erigeron heterochaeta* (Benth. ex C.B. Clarke) Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 388. 1954. *Aster heterochaeta* was a replacement name for *Heterochaeta asteroides* DC.

Aster hedinii Ostenf. in Hedin, S. Tibet 6(3): 37. 1932. **TYPE**: **CHINA**. **Xizang (Tibet)**. SW Tibet, Himalayas norra fot., Från vägen mellan Läger CCIII (Dara-sumkor, 4931 m) och Läger CCIV (Buk-gyäyorap, 4870 m), Mellan båda ligger passet Tugri-la, 5270 m, 16 Jul 1907, *S. Hedin s.n.* (holotype, as annotated on the sheet: S image).

China (Gansu, Qinghai, Sichuan, Xizang, Yunnan), Bhutan, India, Kashmir, Nepal.

3. Tibetiodes bietii (Franch.) Nesom, **comb. nov.** *Aster bietii* Franch., J. Bot. (Morot) 10: 373. 1896. **TYPE**: **CHINA**. **Yunnan**. No other locality data, 3 Jun 1896, *Prince H.* d'Orléans *s.n.* (holotype: P image).

China (Xizang, Yunnan).

4. Tibetiodes brachytricha (Franch.) Nesom, **comb. nov.** *Aster brachytrichus* Franch., J. Bot. (Morot) 10: 372. 1896. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Montagne Hee-chan-men au dessus de Lankong, 11 Jul 1883, *R.P. Delavay 101* (P 711633; isolectotypes: A image, P 711632 image). Protologue: "Yun-nan, in pascuis montis Hee-chan-men supra Lankong (R.P. Delavay n. 101 et 4466); in collibus prope collum Yen-tze-hay, 3200 m (id.)."

Aster bodinieri H. Lév., Bull. Géogr. Bot. 25: 14. 1915. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Plateau du Io-chan, 3400 m, Jun 1914, *E.E. Maire 706* (E 385613; isolectotype: E 385616). Protologue: "Yun-Nan: patures des plateaux et des pics de Ta-Hai, Io-Chan et de Tong-Tchouan."

China (Guizhou, Sichuan, Yunnan), Myanmar.

5. Tibetiodes brevis (Hand.-Mazz.) Nesom, **comb. nov.** *Aster brevis* Hand.-Mazz., Notizbl. Bot. Gart. Berlin-Dahlem. 13: 625. 1937. **TYPE**: **CHINA**. **Yunnan**. Mountains of the Chungtien plateau, SE of Chungtien, stony alpine pasture, 13,000 ft, 15 Jul 1913, *G. Forrest 10516* (holotype: B?; isotype: E image, Fig. 18).

China (Yunnan).

6. Tibetiodes bulleyana (Jeffrey ex Diels) Nesom, **comb. nov.** *Aster bulleyanus* Jeffrey ex Diels, Notes Roy. Bot. Gard. Edinb. 5: 184. 1912. **TYPE**: **CHINA**. **Yunnan**. Western slopes of Kari pass on descent to Shu-pa valley from Pung-tzu-la to Shi-zo, moist shady places, 13,000 ft, 15 Sep 1904, *G. Forrest 7661* (holotype: E image).

China (Yunnan).

7. Tibetiodes diplostephioides (DC.) Nesom, **comb. nov.** *Heterochaeta diplostephioides* DC., Prodr. 5: 282. 1836. *Aster diplostephioides* (DC.) Benth. ex C.B. Clarke, Comp. Ind., 45. 1876. *Erigeron diplostephioides* (DC.) Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 341. 1961. **TYPE**: **KASHMIR**. Cachemire, 1833, *M. Royle 147* (holotype: G-DC image).

Aster delavayi Franch., J. Bot. (Morot) 10: 374. 1896. *Aster diplostephioides* var. *delavayi* (Franch.) Onno, Biblioth. Bot. 106: 69. 1932. *Erigeron delavayi* (Franch.) Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 341. 1961. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Les prairies au col de Yen-tze-hay (Lan Kong), 3200 m, 18 Sep 1885, *J.M. Delavay 1675* (P 711648 image; isolectotypes: P 711649, 711650, 711651, 711661, 711662, and 711663, images). Protologue: "Yun-nan, in pratis supra collum Yen-Tze-hay, alt. 3300 m. (Delavay, n. 1675; 999); Fang-yang-tchang, in pascuis supra Mo-so-yn, alt. 3000 m.)."

Bhutan, China (Gansu, Qinghai, Sichuan, Xizang, Yunnan), India, Kashmir, Nepal, Pakistan.

8. Tibetiodes falconeri (C.B. Clarke) Nesom, **comb. nov.** *Aster diplostephioides* var. *falconeri* C.B. Clarke, Comp. Ind., 45. 1876. *Aster falconeri* (C.B. Clarke) Hutch., Gard. Chron. 47: 398. 1910. *Aster diplostephioides* subsp. *falconeri* (C.B. Clarke) Onno, Bibl. Bot. 106: 69. 1932. *Erigeron falconeri* (C.B. Clarke) Botsch., Acta Inst. Bot. Acad. Sci., U.R.S.S. 21: 341. 1961. **LECTOTYPE** (designated here): **KASHMIR**. "Kashmir," no other collection data, *H. Falconer 561* (K 890378 image; isolectotypes: GOET, K 890379, 890380, and 890382-images, LE, M, P, S, images). Protologue: "An species? coll. Falconeri." Grierson (1964, p. 141) cited "holo.

K" — 890378 is the only one of the K sheets with an institutional label of "Type Specimen" but otherwise it is not distinguished from the others.

Kashmir.

9. Tibetiodes farreri (W.W. Smith & Jeffrey) Nesom, **comb. nov.** *Aster farreri* W.W. Smith & Jeffrey, Notes Roy. Bot. Gard. Edinb. 9: 78. 1916. *Aster diplostephioides* subsp. *farreri* (W.W. Smith & Jeffrey) Onno, Biblioth. Bot. 106: 69. 1932. *Erigeron farreri* (W.W. Smith & Jeffrey) Botsch., Botsch., Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 341. 1961. **LECTOTYPE** (designated here): **CHINA**. **Xizang**. Near Gansu frontier, sporadic in the higher valley fields and alps, in hay grass, 12 Aug 1914, *R. Farrer & W. Purdom 174* (E 385643 image; isolectotype: E 385642 image). The protologue cited only "Farrer and Purdom. No. 174."

Aster nigrotinctus Y. Ling, Contr. Inst. Bot. Natl. Acad. Peiping 2: 461. 1934. *Aster vilmorinii* var. *nigrotinctus* (Y. Ling) Y. Ling, Contr. Inst. Bot. Natl. Acad. Peiping 2: 461. 1934. **LECTOTYPE** (designated here): **CHINA**. **Xizang**. Hsiaowutaishan, 2400 m, 27 Jul 1931, *T.-P. Wang 760* (PE 275522 image; isolectotypes: PE 272528 and 275529 images).

China (Gansu, Hubei, Qinghai, Shanxi, Sichuan).

10. Tibetiodes flaccida (Bunge) Nesom, **comb. nov.** *Aster flaccidus* Bunge, Mém. Acad. Imp. Sci. St.-Pétersbourg Divers Savans 2: 599. 1835. *Erigeron flaccidus* (Bunge) Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 388. 1954. **TYPE**: **RUSSIA**. Protologue: "Hab. in alpinis ad Tschujam et in subalpinis Sailughem; floret Julio mense [perennial]" (Probable type material: P 711768 image, "alp. Tschujae "; possible type material: GH image).

Aster argunensis DC., Prodr. 5: 272. 1836. **TYPE**: **RUSSIA**. Ad fl. Argunum in Dahurie, 1820, *Razgildeev s.n.* (holotype: G-DC image).

Aster glarearum W.W. Smith & Farrer, Notes Roy. Bot. Gard. Edinb. 9: 79. 1916. **TYPE**: **CHINA**. **Gansu.** Kansu, high alpine shingles above Siku, 11,000–12,000 ft, 21 Jun 1914, *R. Farrer and W Purdom 131* (holotype: E image; isotype: E image). f

Bhutan, China (Gansu, Hebei, Qinghai, Shaanxi, Shanxi, Sichuan, Xinjiang, Xizang, Yunnan), India, Iran, Kashmir, Kazakhstan, Mongolia, Nepal, Pakistan, Russia, Uzbekistan.

11. Tibetiodes glandulosa (Keissl.) Nesom, **comb. nov.** *Aster flaccidus* var. *glandulosus* Keissl., Ann. Naturhist. Hofmus. Wien 22: 26. 1907. *Aster glandulosus* (Keissl.) Hand.-Mazz., Ost. Bot. Zeit. 79: 35. 1930 (not *Aster glandulosus* Labill. 1806). *Aster flaccidus* subsp. *glandulosus* (Keissler) Onno, Biblioth. Bot. 26(Heft 106): 66. 1932. **TYPE**: **CHINA**. **Xizang**. Tibet, Sudufer des Mangzaka, 5370 m, Umgebung von Thermen, 1907, *E. Zugmayer s.n.* (holotype: W, photo-E image).

Aster flaccidus var. *fructu-glandulosus* Ostenf. in Hedin, Southern Tibet 6(3): 36. 1922. *Aster flaccidus* subsp. *fructu-glandulosus* (Ostenf.) Onno, Bibl. Bot. 106: 65. 1932. **LECTOTYPE** (designated here): **CHINA**. **Xizang.** Eastern or Inner Tibet, Mandarlik, near Camp XLIV, 5127 m, 18 Aug 1901, *S. Hedin s.n.* (C image; isolectotype: S [as cited by Onno 1932 and by Grierson 1964]). The lectotype comprises the 3 small plants at the bottom right of the sheet; another Hedin collection (2 plants) of the same species is above, another (1 plant) to the left. Protologue: "Northern Tibet, Camp XVII, at a river, 4024 m, 31 Jul 1900 (flow.); Kar-yakak-sai, Camp X, Chimen-tagh, 3984 m, 21 Jul 1900 (flow.); Mandarlik, 3437 m, medio July 1900 (flow.); some spec. very large); Eastern or Inner Tibet, near Camp XLIV, 5127 m, 18 Aug 1901 (flow.); S.W. Tibet, Camp CCXI, East of the lake Manasarovar, 4654 m, 24 Jul 1907 (flow.)."

Ostenfeld (1922) was aware of Keissler's earlier var. *glandulosus* from Tibet but noted that "As nothing is said [in Keissler's protologue] about the achenes I cannot refer it to its proper place and do not know if it is a variety of *A. flaccidus* or of *A. Hedinii* described below."

China (Xizang), India.

12. Tibetiodes himalaica (C.B. Clarke) Nesom, **comb. nov.** *Aster himalaicus* C.B. Clarke, Comp. Ind., 42. 1876. **LECTOTYPE** (designated here): **INDIA**. **Sikkim**. Jongri [Dzongri], 13,000 ft, 15 Oct 1875, *C.B. Clarke 26195* (K 102216 image; isolectotype: K 102214 image). No collections were cited in the protologue. *Clarke 26195* is among sheets with a handwritten label by Clarke as *A. himalaicus*.

Aster mekongensis Onno, Bibl. Bot. 106: 54. 1932. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Lichiang Range, 27° 24' N, stony alpine pasture, 14,000 ft, Sep 1913, *G. Forrest 11137* (E image; isolectotype: PE image-Fig. 25). Without designating a type, Onno cited these collections by Forrest: 11137, 14241, 17230, 18892, 20710, 21984, and 22276, all from herb. E. *Forrest 11137* (E) has Onno's annotation as "Aster mekongensis nova. sp." and matches his description of stems as ca. 15 cm tall. Grierson (1964), followed by Ling (1985) and Chen et al. (2011), cited "Aster mekongensis p.p." as a synonym of both *A. himalaicus* and *A. bietii*.

Bhutan, China (Sichuan, Xizang, Yunnan), India, Myanmar, Nepal.

13. Tibetiodes jeffreyana (Diels) Nesom, **comb. nov.** *Aster jeffreyanus* Diels, Notes Roy. Bot. Gard. Edinb. 5: 185. 1912. **TYPE**: **CHINA**. **Yunnan**. Base of Lichiang peak, Lichiang valley, marshy hillsides, 10,000 ft, Sep 1904, *G. Forrest 669* (holotype: E image-Fig. 25; isotypes: BM image, P image).

China (Guizhou, Sichuan, Yunnan).

14. Tibetiodes labrangensis (Hand.-Mazz.) Nesom, **comb. nov.** *Aster labrangensis* Hand.-Mazz., Notizbl. Bot. Gart. Berlin-Dahlem 13: 621. 1937. *Aster yunnanensis* var. *labrangensis* (Hand.-Mazz.) Y. Ling, Fl. Reipubl. Popularis Sin. 74: 246. 1985. **TYPE**: **CHINA**. **Xizang** (Tibet). Eastern Tibet, grasslands between Labrang and Yellow River, in meadow of Wago (Waro) valley beyond Kadja, 11,500 ft, Jul 1926, *J.F. Rock 14447* (holotype: B not seen; isotypes: E-image, GH image-Fig. 17, W not seen). Protologue: "*Rock 14447*: Herb. Berlin, Mus. Wien."

Aster kawaguchii Kitamura, Acta Phytotax. Geobot. 15: 41. 1953. **TYPE**: **CHINA**. **Xizang** (Tibet). Circa Lhasa, Mt. Cho-mo-sese, 6 Sep 1914, *E. Kawaguchi* (holotype: SM [National Science Museum, Tokyo] 96879, Fig. 4 in the protologue).

China (Gansu, Qinghai, Sichuan, Xizang)

15. Tibetiodes latibracteata (Franch.) Nesom, **comb. nov.** *Aster latibracteatus* Franch., J. Bot. (Morot) 10: 371. 1896. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Lieux frais un peu ombragés, au sommet du Tsang-chan, au dessus de Ta-li, 4000 m, 5 Aug 1884, *R.P. Delavay 1207* (P 11698 image; isolectotypes: K image, P 11697, 11698, and 11699, images). Protologue: "Yun-nan, ad cacumina montis Tsang-chan, alt. 4000 m. (R.P. Delavay, n. 1207, 2650)."

China (Yunnan), Myanmar.

16. Tibetiodes latisquamata (C.E.C. Fischer) Nesom, **comb. nov.** *Doronicum latisquamatum* C.E.C. Fischer, Bull. Misc. Inform. Kew 1937: 98. 1937. *Aster platylepis* Y.L. Chen [nom. nov.], Kew Bull. 39: 159. 1984 (not *Aster latisquamatus* (Maxim.) Hand.-Mazz. 1938). **TYPE**: **INDIA**. **Sikkim**. Tsamgo Lake, common all around lake on rocky shale, 12,000 ft, 3 Aug 1935, *C.S. Cutting and A.S. Vernay 20* (holotype: K image, photo-E!).

Aster heliopsis Grierson, Notes Roy. Bot. Gard. Edinb. 26: 124. 1964. **TYPE**: **NEPAL**. Lihkoo-Shailoong, 14,000-15,000 ft, 1930, *Capt. L. Dhwoj 403* (holotype: E; isotypes: BM-2 images).

China (Xizang), India.

17. Tibetiodes likiangensis (Franch.) Nesom, **comb. nov.** *Aster likiangensis* Franch., J. Bot. (Morot) 10: 370. 1896. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Les hauts côteaux du Li Kiang Suee Chan (Li Kiang), 4000 m, 14 Aug 1886, *R.P. Delavay 2098* (P 711708 image; isolectotypes: A image, P 711706 and 711707 images).

Aster costei H. Lév., Bull. Géogr. Bot. 25: 14. 1915. *Aster likiangensis* subsp. *costei* (H. Lév.) Onno, Biblioth. Bot. 26 (Heft 106): 72. 1932. *Aster asteroides* subsp. *costei* (H. Lév.) Grierson, Notes Roy. Bot. Gard. Edinb. 26: 136. 1964. **TYPE**: **CHINA**. **Yunnan**. Pâtures du Io-Chan, 3300 m, 15 Aug 1912, *E.E. Maire s.n.* (holotype: E image).

Bhutan, China (Sichuan, Xizang, Yunnan).

18. Tibetiodes lipskii (Komarov) Nesom, **comb. nov.** *Aster lipskii* Komarov, Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 2: 8. 1921. Not seen. According to Chen et al. (2011), the original description was based on seeds collected from near Qinghai Hu (Qinghai Province) and cultivated at the Komarov Botanical Gardens. Treated as a good species by Ling (1985) and by Chen et al. (2011). Two collections from the region of the type locality are morphologically distinctive and have been identified as *Aster lipskii*: **Gansu**. Lapuleng, weedy slope, 3800 m (12,500 ft), 19 Jul 1937, *T.-P. Wang 7256* (PE, Fig. 14). **Qinghai**. Halihatu Mountain, Xireg, Ulan County, Chaidamu Basin, 26 Jul 1956, *Qinghai Collecting Team 642* (PE, Fig. 15).

China (Gansu, Qinghai).

19. Tibetiodes nepalensis (Grierson) Nesom, **comb. et stat. nov.** *Aster falconeri* subsp. *nepalensis* Grierson, Notes Roy. Bot. Gard. Edinb. 26: 141. 1964. **LECTOTYPE** (designated here): **NEPAL**. Bhurchula Lekh, near Jumla, open slopes among dwarf rhododendrons, 12,500 ft, 11 Jul 1952, *O. Polunin, W.R. Sykes, and L.H.J. Williams 4554* (E image; isolectotype: BM, as cited by Grierson). Grierson did not designate a type but cited many collections from Kumaun (India) and Nepal.

India, Nepal.

20. Tibetiodes retusa (Ludlow) Nesom, **comb. nov.** *Aster retusus* Ludlow, Bull. Brit. Mus. (Nat. Hist.), Bot. 2: 69. 1956. **TYPE**: **CHINA**. **Xizang.** SE Tibet, Kungbo, Nambu La, on rocks, 14,000 ft, 18 Jul 1947, *F. Ludlow & G. Sherriff 15467* (holotype: BM image).

China (Xizang).

21. Tibetiodes salwinensis (Onno) Nesom, **comb. nov.** *Aster salwinensis* Onno, Biblioth. Bot. 26 (Heft 106): 74, pl. IB. 1932. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. No other locality data, 1917-1919, *G. Forrest 19088* (K 890445 image, Fig. 22). There are 7 other K collections by Forrest with the same minimal label data, each with a different collection number, each with a handwritten annotation by Onno in 1930 as "Aster salwinensis Onno nova sp."

China (Sichuan, Xizang, Yunnan), Myanmar. Phyllary morphology of *T. salwinensis* (Figs. 12A, 22) is unusual, as are the relatively broad, few ray flowers in a single series. But morphology otherwise seems characteristic of the genus and molecular data place it there.

22. Tibetiodes setchuenensis (Franch.) Nesom, **comb. nov.** *Aster setchuenensis* Franch., J. Bot. (Morot) 10: 377. 1896. **TYPE**: **CHINA**. **Sichuan**. "Thibet Oriental, Ta-tsien-lou (Principauté de Kiala)," 1893, *J.-A. Soulié 472* (holotype: P image).

China (Sichuan).

23. Tibetiodes stracheyi (Hook. f.) Nesom, **comb. nov.** *Aster stracheyi* Hook. f., Fl. Brit. India 3(8): 250. 1881. **LECTOTYPE** (designated here): **INDIA**. **Uttarakhand**. Kumaon, Pindari, 12,000 ft, 1848, *R. Strachey & J.E. Winterbottom* 2 (K 890386 image; isolectotypes: BM, K, P, images). Protologue: "WESTERN ALPINE HIMALAYA; Kumaon, *Wallich*; Pindari, alt. 12,000 ft., *Str. & Wint.*, *Stewart*."

Bhutan, China (Xizang), India, Nepal.

24. Tibetiodes techinensis (Y. Ling) Nesom, **comb. nov.** *Aster techinensis* Y. Ling, Fl. Reipubl. Pop. Sin. 74: 359. 1985. **TYPE**: **CHINA**. **Yunnan**. Y. Atuntze, Yangtsatung, 3900 m, 24 Aug 1938, *T.T. Yü 9828* (holotype: PE 275892 image; isotypes: A image, KUN image, PE-5 sheets images).

China (Yunnan).

25. Tibetiodes tientschwanensis (Hand.-Mazz.) Nesom, **comb. nov.** *Aster tientschwanensis* Hand.-Mazz., Oesterr. Bot. Zeit. 89: 58. 1940. **TYPE**: **CHINA**. **Sichuan**. Tien-chuan-hsien, 3340 m, 13 Jun 1936, *K.L. Chu* 2780 (holotype: B?; isotypes: E image, PE image).

China (Sichuan).

26. Tibetiodes tsarungensis (Grierson) Nesom, **comb. nov.** *Aster flaccidus* subsp. *tsarungensis* Grierson, Notes Roy. Bot. Gard. Edinburgh 26: 133. 1964. *Aster tsarungensis* (Grierson) Y. Ling, Fl. Reipubl. Popularis Sin. 74: 241. 1985. **TYPE**: **CHINA**. **Xizang** (Tibet). Doker La, 28 20'N, 3960 m Aug 1918, *G. Forrest 16873* (holotype: E image-Fig. 19).

China (Sichuan, Xizang, Yunnan).

27. Tibetiodes yunnanensis (Franch.) Nesom, **comb. nov.** *Aster yunnanensis* Franch., J. Bot. (Morot) 10: 375. 1896. *Aster diplostephioides* var. *yunnanensis* (Franch.) Onno, Biblioth. Bot. 106: 69. 1932. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Les bois de Fang-yang-tchang, 3000 m, 19 Jul 1887, *R.P. Delavay 3107* (P 711811 image; isolectotypes: K image, P 711814 and 711815 images). Protologue: "Likiang in pratis et silvis haud procul a nivibus perpetuis, alt. 3500 m. (Delavay, n. 2099 et 2482);" in silvis ad Kan-ho, prope Fang-yang-tchang, alt. 3000 m. (id., n. 3107 et 3701; ad collum Lo-pin-chan (id.)."

Aster vilmorinii Franch., J. Bot. (Morot) 10: 373. 1896. *Erigeron vilmorinii* (Franch.) Botsch., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 21: 342. 1961. **LECTOTYPE** (designated here): **CHINA**. **Sichuan**. Ta-tsien-lou, 17 Jun 1891, *M. Pratt 631* (P 7111807 image; isolectotype: BM image). Protologue: "Se-tchuen occid., in silvis prope Ta-tsien-lou (R.P. Soulié, n. 418; Pratt, n. 631; Tongolo ad limites tibetana, in quercetis et betuletis (id., n. 505)."

China (Sichuan, Yunnan).

ACKNOWLEDGEMENTS

Thanks to Dave Boufford (Harvard University Herbaria) for help in interpreting Chinese names and geography. Photos by David Bouffourd and Susan Kelley are from the "Biodiversity of the Hengduan Mountains and adjacent areas of south-central China" website.

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Figure 2. *Tibetiodes diplostephioides*. Sichuan. Photo by Dave Boufford, 2005.

Figure 3. *Tibetiodes diplostephioides*. St. Andrews Botanic Garden. Photo by Kirsty Wilson, 2010.

Figure 4. *Tibetiodes yunnanensis*. Sichuan. Photo by Susan Kelley, 2006.

Figure 5. *Tibetiodes yunnanensis*. Sichuan. Photo by Susan Kelley, 2006.

Figure 6. *Tibetiodes labrangensis*. Tibet. Photo by Dave Boufford, 2004.

Figure 7. *Tibetiodes flaccidus*. Sikkim. Photo by Harry Jans, 2018, iNaturalist.

Nesom: *Tibetiodes*, gen. nov.

Figure 8. *Tibetiodes flaccidus*. Yunnan. Photo by Dave Boufford, 2013.

Figure 9. *Tibetiodes himalaicus*. Nepal. Photo by T. Abe Lloyd, 2017.

Figure 10. *Tibetiodes* involucres. A. *T. stracheyi*. B. *T. latisquamatum*. C. *T. brachytricha*. D. *T. himalaica*. E. *T. jeffreyana*. F. *T. yunnanensis*.

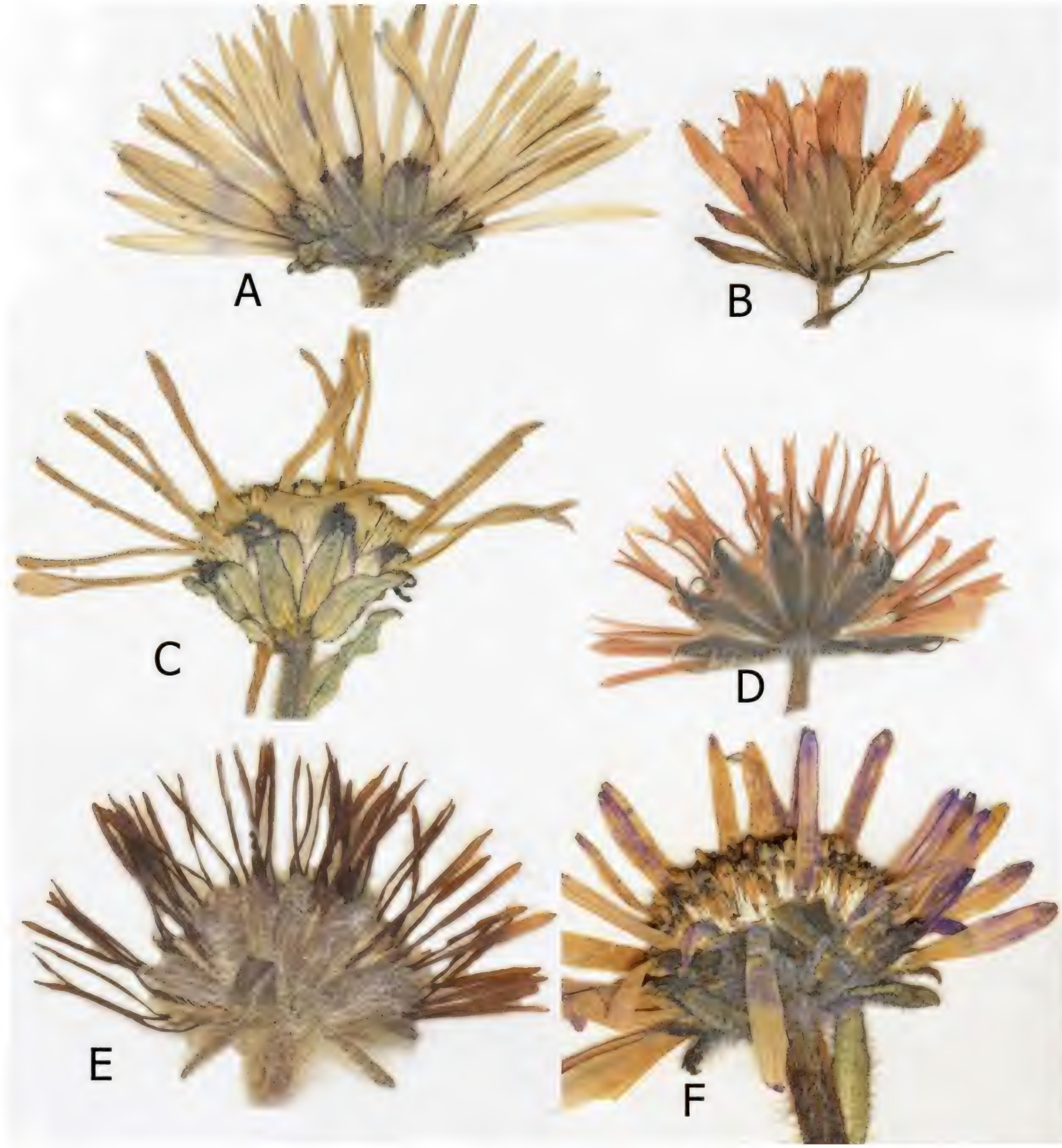

Figure 11. *Tibetiodes* involucres. A. *T. likiangensis* B. *T. tientschwanensis*. C. *T. retusa*. D. *T. asteroides*. E. *T. flaccidus*. F. *T. brevis*.

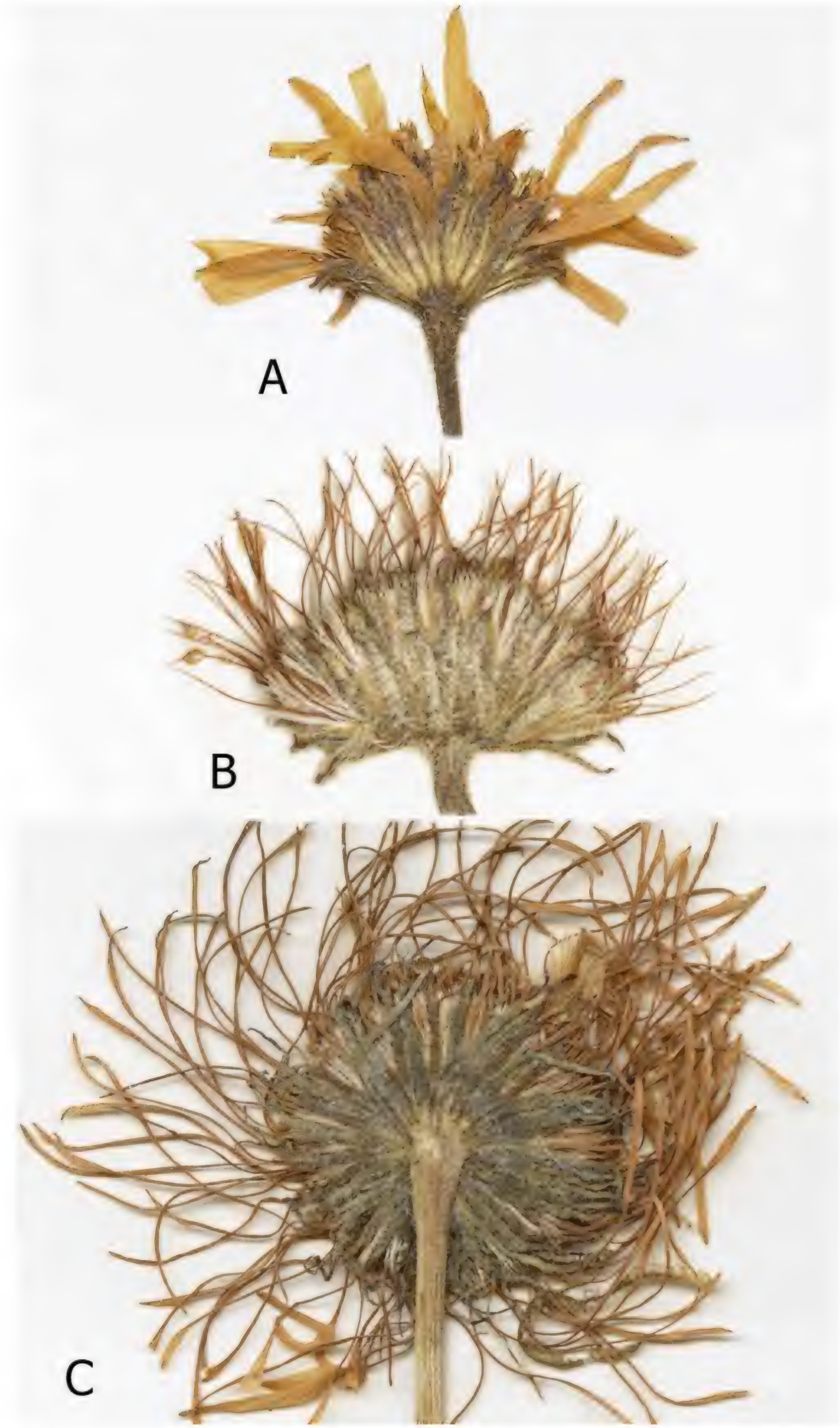

Figure 12. *Tibetiodes* involucres. A. *T. salwinensis.* B. *T. labrangensis*. C. *T. farreri*.

Nesom: *Tibetiodes*, gen. nov.

Figure 13. *Tibetiodes diplostephioides*. Yunnan. *Forrest 30624* (E).

Figure 14. *Tibetiodes lipskii*. Gansu. *Wang 7256* (PE).

Figure 15. *Tibetiodes lipskii*. Qinghai. *Qinghai Collecting Team 642* (PE).

Nesom: *Tibetiodes*, gen. nov.

Figure 16. *Tibetiodes bietii*. Yunnan. *Rock 9728* (E).

Nesom: *Tibetiodes*, gen. nov.

Figure 17. *Tibetiodes labrangensis*. Tibet. *Rock 14447*, isotype (GH).

Nesom: *Tibetiodes*, gen. nov.

Figure 18. *Tibetiodes brevis*. Yunnan. *Forrest 10516*, asdfafd, *Aster brevis* (E).

Figure 19. *Tibetiodes tsarungensis*. Yunnan. *Forrest 16873*, *Aster flaccidus* subsp. *tsarungensis*, holotype (E).

Figure 20. *Tibetiodes asteroides*. Tibet. *Lepcha 226* (K).

Nesom: *Tibetiodes*, gen. nov.

Figure 21. *Tibetiodes likiangensis*. Yunnan. *Forrest 6001* (E).

Nesom: *Tibetiodes*, gen. nov.

Figure 22. *Tibetiodes salwinensis*. Yunnan. *Forrest 19088*, lectotype (K).

Figure 23. *Tibetiodes stracheyi*. Nepal. *Hoshino et al. 9666126* (E).

Nesom: *Tibetiodes*, gen. nov.

Figure 24. *Tibetiodes brachytricha*. Yunnan. *Rock 9728* (US).

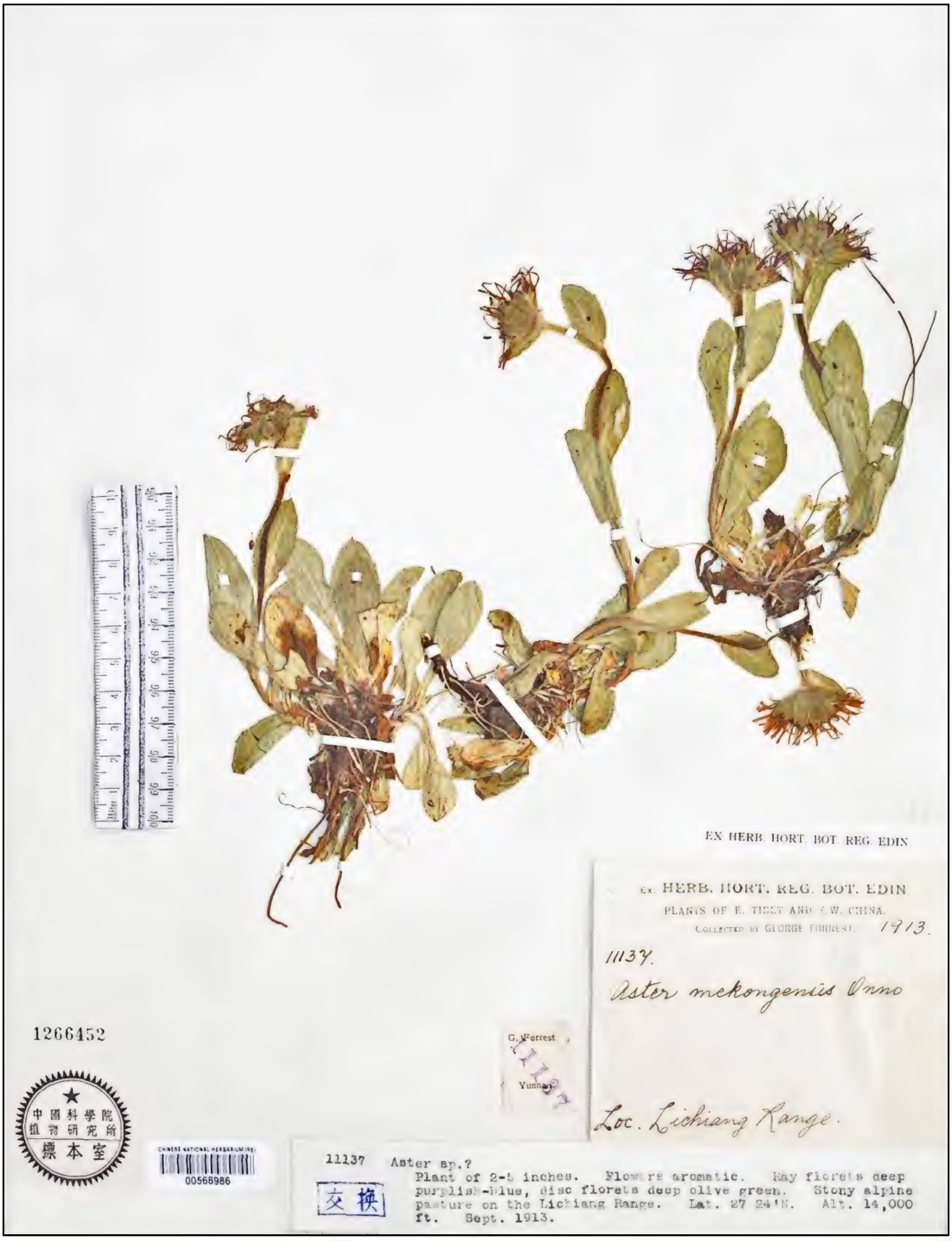

Figure 25. *Tibetiodes himalaicus*. Yunnan. *Forrest 11134*, isolectotype of *Aster mekongensis* (PE).

Figure 26. *Tibetiodes jeffreyana*. Yunnan. *Forrest 669*, holotype of *Aster jeffreyanus* (E).

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NEW GENERA FROM ASIAN *ASTER* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Four new genera of Astereae subtribe Asterinae are described, based on species segegated from southeast Asian *Aster*. **Geothamnus** Nesom, **gen. nov.**, includes the single species ***Geothamnus batangensis*** (Bureau & Franch.) Nesom, **comb. nov.** **Iteroloba** Nesom, **gen. nov.**, includes the single species ***Iteroloba bipinnatisecta*** (Ludlow ex Grierson) Nesom, **comb. nov.** **Sinosidus** Nesom, **gen. nov.**, includes ***Sinosidus albescens*** (DC.) Nesom, **comb. nov.** (incl. 10 varieties), ***Sinosidus argyropholis*** (Hand.-Mazz.) Nesom, **comb. nov.**, ***Sinosidus fulgidulus*** (Grierson) Nesom, **comb. nov.**, ***Sinosidus hypoleucus*** (Hand.-Mazz.) Nesom, **comb. nov.**, ***Sinosidus lavandulifolius*** (Hand.-Mazz.) Nesom, **comb. nov.**, ***Sinosidus motuoensis*** (Y.L. Chen) Nesom, **comb. nov.**, ***Sinosidus paradoxus*** (Y. Ling) Nesom, **comb. et stat. nov.**, and ***Sinosidus polius*** (C.K. Schneid.) Nesom, **comb. nov.** **Griersonia** Nesom, **gen. nov.**, includes ***Griersonia fuscescens*** (Bureau & Franchet) Nesom, **comb. nov.**, ***Griersonia oblongifolia*** (Grierson) Nesom, **comb. nov.**, and ***Griersonia senecioides*** (Franch.) Nesom, **comb. nov.** Formal typification/synonymy and illustrations are provided. Lectotypes are designated for *Amphirhapis albescens*, *Aster lavandulifolius*, and *Aster staticifolius*.

Molecular-phylogenetic data and morphology indicate that various species of southeast Asian *Aster* are outside the bounds of those currently to be treated as *Aster* sensu stricto (summaries in Nesom 2020a, 2020b). Of the four new genera described here, the segregation of three is supported by molecular and morphological data; the fourth (*Iteroloba*) has not been sampled molecularly and its recognition is based on its morphological isolation.

GEOTHAMNUS Nesom, **gen. nov.** **TYPE:** *Geothamnus batangensis* Nesom

Distinct in its low, caespitose habit from a woody taproot and subterranean, branching caudex, glandular stems and punctate leaf surfaces, leaves basal and lower cauline, solitary heads on subscapose stems, phyllaries relatively few, essentially linear, evenly thin-herbaceous, and equal-length, and thick-ribbed achenes with a multiseriate pappus of clavate-tipped bristles.

Geothamnus batangensis (Bureau & Franch.) Nesom, **comb. nov.** *Aster batangensis* Bureau & Franch., J. Bot. (Morot) 5: 50. 1891. **TYPE**: **CHINA**. **Sichuan**. "Se-Tchuen, entre Batang et Litang, 14 Jun 1890, *P.G.E. Bonvalot s.n.* with Prince Henri d'Orléans (holotype: P 00711628 image!; isotypes: P-2 sheets images!). Protologue: "Sur les montagnes entre Batang et Litang."

Aster staticifolius Franch. [as "staticefolius"], J. Bot. (Morot) 10: 370. 1896. *Aster batangensis* var. *staticifolius* (Franch.) Y. Ling, Fl. Reipubl. Popularis Sin. 74: 253. 1985. **LECTOTYPE** (designated here): **CHINA**. **Yunnan**. Les roches calcaires au dessus du Col de Yen-tze-hay (Lankong), 3500 m, 8 Jul 1886, *J.M. Delavay 157* (P 00711766 image!, photo-E!; isolectotypes: K-Fig. 2, P 0071165, A-photo and fragment of P 0071175).

Protologue: "Likiang ad rupes sub nivibus perpetuis (Delavay, n. 157); Hokin, supra collum Koua-la-po, alt. 3200 m (id.); ad collum Yen-tze-hay, (id.)." Other syntypes are at P: *Delavay*, 13 Jul 1886 (P 00711762); *Delavay*, 18 Sep 1883 (P 00711764); *Delavay*, 9 Jul 1884 (P 00711768)

Low subshrubs to perennial caespitose herbs from a woody taproot and branching caudex with rhizome-like branches; stems, peduncles, leaves, and involucres stipitate- or punctate-glandular. **Stems** scapiform, 3–15 cm tall, stipitate-glandular and strigose-hirsute. **Leaves** basal and lower cauline, obovate to oblanceolate, reduced to bracts on the distal half of the stem, margins entire, surfaces weakly punctate-

glandular, otherwise glabrate to sparsely hirsute-strigose. **Heads** terminal, solitary. **Involucres** broadly campanulate, 10–15 mm wide (pressed); epaleate; phyllaries in (1–)2(–3) subequal series, narrowly oblong-lanceolate to elliptic-lanceolate, loose and spreading, evenly thin-herbaceous, inner scarious and sometimes with a green apical patch, minutely stipitate glandular, otherwise glabrous to hirsute-strigose. **Ray florets** 12–26, ligules 12–22 mm long, purple to lavender-blue, not coiling. **Disk flowers** bisexual, fertile, corollas narrowly funnelform, 3.2–3.5 mm, lobes deltate-triangular, equal-length; anther thecae without tails, apical appendages broadly lanceolate and prominent. **Achenes** narrowly obovoid, compressed, 3.5–4 mm long, strigose-sericeous, eglandular, each margin and one of the faces with a thickened rib; pappus multiseriate, outermost series of short scales, inner of coarsely barbellate bristles 2–3 mm increasing in length to 5–5.5 mm, innermost weakly clavate at the apex.

Forest and thicket margins, openings in oak-spruce and spruce-fir forests, meadows, gravelly, stony, or scree slopes, cliff faces and ledges, stream banks and around seepages and streamlets, grazed pastures with juniper; 2500–4600 m. Southwestern and western Sichuan, eastern Xizang, northwestern Yunnan (mostly from Flora of China).

Geothamnus batangensis (as *Aster*) keys in the Flora of China (Chen et al. 2011) with *Aster* sect. *Alpigeni* because of its basal rosette, solitary heads on scapose stems, and equal-length phyllaries, but it differs from all of these species in its taprooted habit, without stolons or rhizomes but becoming caespitose through woody, rhizome-like caudex branches. Secondary growth of the caudex branches sometimes is pronounced, sometimes to the point of a cork-like outer layer and such features suggest that the ancestry of *G. batangensis* is with shrubby species. In combination with its solitary heads, glandular vestiture, and multiseriate pappus, this species is isolated among Asian Astereae and is segregated here at generic rank. Phylogenetic analyses based on molecular data (e.g., Li et al. 2012; Fu et al. 2019) show it in an unresolved position among species and species groups, apparently near *Myriactis*, placed by Nesom (2020a, 2020b) in the Asterothamnus branch of subtribe Asterinae.

Aster staticifolius was described by Franchet as differing from *Aster batangensis* in its less densely hairy stems, leaves, and phyllaries; Chen et al. (2011) recognized it at varietal rank, emphasizing the vestiture, but the two varieties as so identified are more or less congruent in geography and it seems likely that the variation in vestiture is populational rather than marking distinct evolutionary entities.

Figure 1. *Geothamnus batangensis*. Detail from *Delavay s.n.* (P 711762, syntype of *Aster staticifolius*)

Figure 2. *Geothamnus batangensis*. *Delavay 157* (K [ex P], isolectotype of *Aster staticifolius*).

Figure 3. *Geothamnus batangensis*. Sichaun, *Rock 17844* (US).

Figure 4. *Geothamnus batangensis*. Sichuan, *Kunming & Edinburgh Exped. 217* (E).

Figure 5. *Geothamnus batangensis*. Top and bottom: Sichuan, 15 July 2004. Photographs by Dave Boufford.

ITEROLOBA Nesom, **gen. nov.** **TYPE**: *Iteroloba bipinnatisecta* (Ludlow ex Grierson) Nesom

Distinct among Asian species in its low, perennial habit from a short, thick, woody taproot, basal rosette of bipinnatisect leaves, solitary heads on leafy stems, scarious phyllaries in 2(–3) series of equal length, bisexual disc flowers, and small achenes.

Iteroloba bipinnatisecta (Ludlow ex Grierson) Nesom, **comb. nov.** *Aster bipinnatisectus* Ludlow ex Grierson, Notes Roy. Bot. Gard. Edinb. 26: 144. 1964. **TYPE**: **CHINA**. **Xizang** (Tibet Autonomous Region). Xoka, "SE Tibet, Kongbo, Shoga Kong, 30° 00' N, 93° 48' E, rock faces, 10,500 ft," 20 Jul 1947, *F. Ludlow, G. Sherriff, and H.H. Elliot 14164* (holotype: BM, Figs. 1-4).

Perennial herbs from a thick, woody taproot, stem and leaves sparsely but prominently villous with loose white hairs 1–2 mm long, eglandular. **Stems** 2–8 cm tall, unbranched, arising from the multicipital caudex or very short caudex branches. **Leaves** basal and cauline, bipinnatisect, primary lobes 3–5 pairs, each with 3–8 pairs of linear, apiculate-tipped secondary segments 1–3 cm long; basal dense, blades 1–2 cm long, with a narrow petiole 1–2 cm long, base of petiolate dilated and clasping, old leaf bases and petioles persisting; cauline bipinnatisect but epetiolate and diminishing in size from the basal, continuing nearly to the heads. **Heads** solitary on leafy stems. **Involucres** 12–15 mm wide (pressed); phyllaries in 2(–3) series of equal length, linear-oblong to linear-oblanceolate or -lanceolate, thin, proximally stramineous with scarious margins, herbaceous and sometimes purplish on distal half, villous, eglandular. **Ray flowers** 20–35, tube 2.5–3 mm long, ligules 13–15 mm long, ca. 2 mm wide, "very pale mauve" (pale purple with a gray tint), not coiling. **Disc flowers** apparently bisexual and fertile, yellow, corollas narrowly funnelform-tubular, 5.5–6 mm long, lobes deltate-triangular, 1 mm long. **Achenes** ca. 1.5 mm long; pappus of slender, barbellate, acute-tipped bristles in 2 series, inner about as long as the disc corollas, outer ca. 1 mm long.

Apparently known only from the type collection.

As noted by Chen et al. (2011) these plants are distinct among Asian *Aster* in their repeatedly divided leaves in rosettes at the base of woody stems. The isolated position of *Iteroloba bipinnatisecta* shown in the phylogenetic arrangement of the subtribe (Fig. 1 in Nesom 2020a, 2020b) is speculative, even its placement as a member of subtribe Asterinae.

The mostly scarious phyllaries and the small achenes of *Iteroloba bipinnatisecta* are similar to those of *Erigeron*, but native Eurasian erigerons are relatively uniform in habit — with oblanceolate leaves often in a rosette from a fibrous-rooted rhizome — and probably are derived from a single (North American) lineage (e.g., Huber & Nilsson 1995; Farhani 2018). The short, thick, woody, taproot of *I. bipinnatisecta* is anomalous among Eurasian *Erigeron* — it suggests that the relationship of *Iteroloba* might be closer to *Psychrogeton* (Asterinae), which also is woody-taprooted with a basal rosette and solitary heads (although *Psychrogeton* characteristially has undivided leaves and functionally staminate disc flowers). Plants of *Chlamydites* also are monocephalous and produce a branching system of rhizomes but they apparently are not taprooted. For an alternative hypothesis evolutionarily and geographically further out, perhaps the ancestor of *Iteroloba* is from subtr. Brachyscominae.

Figure 1. *Iteroloba bipinnatisecta*, holotype.

Figure 2. *Iteroloba bipinnatisecta*, single plant from holotype.

Figure 3. *Iteroloba bipinnatisecta*, details from holotype

Figure 4. *Iteroloba bipinnatisecta*, detail from holotype. Flat, epaleate receptacle and narrow, mostly scarious phyllaries in 2(–3) series of equal length.

SINOSIDUS Nesom, **gen. nov.** **TYPE:** *Sinosidus albescens* (DC.) Nesom
Aster ser. *Albescentes* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 357, 179. 1985.

Distinct in their shrubby habit, leaves often closely gray- to white-tomentose abaxially and often sessile-glandular, relatively small, few-rayed heads in corymbs, keeled phyllaries in 4–5 strongly graduate series, and terete, multi-nerved achenes with apically clavate pappus bristles.

Shrubs. **Stems** many-branched, 0.2–3(–4) m. **Leaves** cauline, sessile to short-petiolate, blades broadly ovate to elliptic, oblong, lanceolate, or linear 0.5–8(–20) cm long, margins flat to revolute, entire to remotely apiculate, serrulate, or coarsely serrate, closely gray- to white-tomentose abaxially or sometimes glabrous, sometimes glandular beneath the tomentum with sessile, resinous glands, venation camptodromous to subbrochidodromous. **Heads** in terminal, corymboid clusters, the clusters often compound (clusters of clusters), heads rarely few or solitary (*S. polius*, *S. hypoleucus*), peduncles bracteate 5–50 mm long. **Involucres** campanulate to cylindric, 5–9 mm wide (pressed); phyllaries in 4–5 strongly graduate series, ovate-lanceolate to lanceolate, keeled (midvein distally swollen), outer distally green, proximally stramineous, margins scarious; receptacles epaleate. **Ray flowers** (4–)8–25, ligules 2–7 mm long, white to pale violet, pink, or purple, not coiling. **Disk flowers** bisexual, fertile, 4–6 mm long, lobes triangular, 1–2 mm long and recurving-coiling or sometimes shorter and somewhat erect, eglandular or glandular; anther thecae without tails. **Achenes** fusiform to narrowly obovoid, terete to slightly compressed, 1.5–3 mm long, 4–8-nerved, glabrate to short-strigose, eglandular or minutely glandular, the glands caducous but visible at least before fruit maturity; pappus of barbellate bristles, inner half the length to as long as the disc corollas, innermost with clavate tips, outer of setae 0.2–1 mm long.

The genus *Amphirhapis* was established by deCandolle (1836), with no type cited, as comprising six species — *A. albescens*, *A. cuspidata*, *A. heterotricha*, *A. peduncularis*, *A. pubescens*, and *A. rubricaulis*. *Amphirhapis albescens* (with "Wall. cat. n. 2974. comp. n. 84") cited in synonymy, was transferred to *Aster* by Handel-Mazetti in 1938 as *Aster albescens* (DC.) Wall. ex Hand.-Mazz. Nees in 1832 had earlier described *Aster peduncularis* Wall. ex Nees, the same species as de Candolle's *Amphirhapis peduncularis* and based on the same Wallich collection — now treated as *Cordiofontis peduncularis* (Nees) Nesom. Jeffrey (1982), however, typified *Amphirhapis* with *A. heterotricha* DC., synonym of a species now treated in the genus *Duhaldea* of the Inuleae (Anderberg 1991).

Recognition of these species at generic rank was suggested by Nesom (1994), based on morphology. Molecular-phylogenetic analyses (Li et al. 2012; Zhang et al. 2015; Fu et al. 2019) indicate that they comprise a monophyletic group in the Psychrogeton branch of Asterinae (Nesom 2020a, 2020b).

The species of *Sinosidus* vary greatly among themselves in leaf morphology. Formally described variants of *S. albescens* need taxonomic study, as does the whole genus.

1. **Sinosidus albescens** (DC.) Nesom, **comb. nov.** *Amphirhapis albescens* DC., Prodr. 5: 343. 1836. *Microglossa albescens* (DC.) C.B. Clarke, Comp. Ind., 59. 1876. *Aster albescens* (DC.) Wall. ex Hand.-Mazz., Acta Horti Gothob. 12: 205. 1938. **LECTOTYPE** (designated here): **NEPAL**. "In Nepalia ad Kamaon et Gossain-Than, in Hb. 1824, N. *Wallich 2974/84* (K-Wallich). DeCandolle also cited *Wallich 3066/176*, identified by Wallich as "Solidago salicifolia" but also a collection of *Sinosidus albescens*.

Aster albescens is "a variable complex of intergrading populations of shrubs that extend from the western Himalaya to central and south-central China. Ten varietal names have been assigned to segregates of this complex in China, based primarily on pubescence, gland characters, and size of the leaves, and pubescence and shape of the involucres" (Boufford & Chen 2009). Ten infraspecific taxa are recognized in the recent Flora of China treatment (Chen et al. 2011) — no attempt is made here to evaluate their evolutionary validity.

a. **Sinosidus albescens** var. **albescens** *Aster albescens* var. *albescens*

b. **Sinosidus albescens** var. **discolor** (Y. Ling) Nesom, **comb. nov.** *Aster albescens* var. *discolor* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 358. 1985. **TYPE**: **Sichuan**. *Wang 7896*.

c. **Sinosidus albescens** var. **glandulosus** (Hand.-Mazz.) Nesom, **comb. nov.** *Aster albescens* var. *glandulosus* Hand.-Mazz., J. Bot. (Morot) 76: 284. 1938. **TYPE**: **Xizang**. *Chamdo 10752*.

d. **Sinosidus albescens** var. **gracilior** (Hand.-Mazz.) Nesom, **comb. nov.** *Aster albescens* var. *gracilior* (Hand.-Mazz.) Hand.-Mazz., Acta Horti Gothob. 12: 206. 1938. *Aster limprichtii* var. *gracilior* Hand.-Mazz., Symb. Sin. 7: 1093. 1936. **TYPE**: **Sichuan**. *Handel-Mazzetti 7350*.

e. **Sinosidus albescens** var. **glabratus** (Diels) Nesom, **comb. nov.** *Aster albescens* var. *glabratus* (Diels) Boufford & Y.S. Chen, Harvard Pap. Bot. 14: 43. 2009. *Aster harrowianus* var. *glabratus* Diels, Notes Roy Bot. Gard. Edinb. 5: 184. 1912. **TYPE**: **Yunnan**. *Forrest 2508*. Synonym: *Aster albescens* var. *levissimus* Hand.-Mazz.

f. **Sinosidus albescens** var. **limprichtii** (Diels) Nesom, **comb. nov.** *Aster albescens* var. *limprichtii* (Diels) Hand.-Mazz., Acta Horti Gothob. 12: 206. 1938. *Aster limprichtii* Diels, Repert. Spec. Nov. Regni Veg. Beih. 12: 503. 1922. **TYPE**: **Xizang**. *Limpricht 2226*.

g. **Sinosidus albescens** var. **megaphyllus** (Y. Ling) Nesom, **comb. nov.** *Aster albescens* var. *megaphyllus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 358. 1985. **TYPE**: **Sichuan**. *Z. He and Z.L. Zhou 13318*.

h. **Sinosidus albescens** var. **pilosus** (Hand.-Mazz.) Nesom, **comb. nov.** *Aster albescens* var. *pilosus* Hand.-Mazz., Acta Horti Gothob. 12: 207. 1938. **TYPE**: **Yunnan**. *Rock 5164*.

i. **Sinosidus albescens** var. **rugosus** (Y. Ling) Nesom, **comb. nov.** *Aster albescens* var. *rugosus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 358. 1985. **TYPE**: **Sichuan**. *Soulie 1893*.

j. **Sinosidus albescens** var. **salignus** (Franch.) Nesom, **comb. nov.** *Aster albescens* var. *salignus* (Franch.) Hand.-Mazz., Acta Horti Gothob. 12: 207. 1938. *Inula cuspidata* var. *saligna* Franch., Nouv. Arch. Mus. Hist. Nat., sér. 2, 10: 37. 1888. **TYPE**: **Xizang**. *J.P.A. David s.n.*

2. **Sinosidus argyropholis** (Hand.-Mazz.) Nesom, **comb. nov.** *Aster argyropholis* Hand.-Mazz., Acta Horti Gothob. 12: 208. 1938. **TYPE**: **CHINA**. **Sichuan**. Szechuan bor., Tatien, frutex fere metralis in declivo aprico, 2 Jul 1922, *H. Smith 2258* (UPS, Fig. 7).

Aster argyropholis var. *niveus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 358. 1985. **CHINA**: **Sichuan**. Descending to Li-fan Hsien, roadside, 2700 m, 8 Jul 1930, *F.T. Wang 21626* (holotype: PE image, Fig. 8).

Among numerous collections of *Aster argyropholis* (PE), the distinction of var. *niveus* seems arbitrary. *Aster argyropholis* var. *paradoxus* (below) is distinctive and apparently known only from the type collection.

3. **Sinosidus paradoxus** (Y. Ling) Nesom, **comb. et stat. nov.** *Aster argyropholis* var. *paradoxus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 358. 1985. **CHINA**. **Sichuan**. Ma-er-kang (Barkam) (Marcon), 2700 m, 18 Jul 1951, *C. Li 23091* (holotype: PE image, Fig. 12; isotype: KUN image, Fig. 13).

4. **Sinosidus fulgidulus** (Grierson) Nesom, **comb. nov.** *Aster fulgidulus* Grierson, Notes Roy. Bot. Gard. Edinb. 26: 110. 1964. **TYPE**: **CHINA**. **Xizang**. Southeast Tibet, Tangme, Po Tsangpo-Yirong [confluence], 7000 ft, 3 Jun 1947, *F. Ludlow, G. Sherriff, and H.H. Elliot 13074* (holotype: E image, Fig. 14; isotype: BM).

5. **Sinosidus hypoleucus** (Hand.-Mazz.) Nesom, **comb. nov.** *Aster hypoleucus* Hand.-Mazz., J. Bot. British and Foreign 76: 285. 1938. **TYPE**: **CHINA**. **Xizang**. Kyimdong Dzong, an undershrub

of the hot cliffs, 11,000-12,000 ft, 14 Jul 1935, *F. Kingdon-Ward 11993* (holotype: BM image, Fig. 15).

Wang et al. (2019) have characterized the chloroplast genome of *Sinosidus hypoleucus*.

6. **Sinosidus lavandulifolius** (Hand.-Mazz.) Nesom, **comb. nov.** *Aster lavandulifolius* Hand.-Mazz., Notizbl. Bot. Gart. Berlin-Dahlem. 13: 609. 1937. **LECTOTYPE** (designated here): **CHINA**. **Sichuan**. Plants of the Muli Kingdom, watershed of the Shou-Chu River and Shou-Chu Valley, in dry gorge, 2435-2900 m, Jun 1928, *J.C.F. Rock 16273* (W; isolectotype: US, Fig. 16). The protologue cited duplicates from B and W.

7. **Sinosidus motuoensis** (Y.L. Chen) Nesom, **comb. nov.** *Aster motuoensis* Y.L. Chen, Bull. Bot. Res., Harbin 8: 12. 1988. **TYPE**: **CHINA**. **Xizang**. Motuo, in prato lapidoso secus marginem rivuli, 1100 m, Dec 1982, S.*Z. Cheng & B.S. Li 2181* (holotype: PE, Fig. 17).

8. **Sinosidus polius** (C.K. Schneid.) Nesom, **comb. nov.** *Aster polius* C.K. Schneid. in Sargent, Pl. Wilson. 3: 459. 1917. **TYPE**: **CHINA**. **Sichuan**. Western Szech'uan, near Monkong Ting, valley of Hsiao-chin Ho, 2200-2700 m, Jun 1908, *E.H. Wilson 2233* (holotype: A; isotype: US image, Fig. 18).

Fu et al. (2019) have provided a detailed update on *Aster polius*, with a description, phylogenetic analysis, drawings, and photographs. They note that *Sinosidus polius* is known only from rocky slopes in a restricted area of Xiaojin County, Sichuan.

Figure 1. *Sinosidus albescens*. Sichuan. Photo by Susan Kelley, "Biodiversity of the Hengduan Mountains" website.

Figure 2. *Sinosidus albescens*. Valley of Flowers, Uttarakhand, India. Photo by Thingnam Girija, "Flowers of India" website.

Figure 3. *Sinosidus albescens*. Tibet. Photo by Bruce Bartholomew, "Biodiversity of the Hengduan Mountains" website.

Figure 4. *Sinosidus albescens*. Nepal, *DNEP3 BY4* (E).

Figure 5. *Sinosidus albescens*. Yunnan, *1984 Sino-Amer. Bot. Exped. 1211* (US).

Figure 6. *Sinosidus albescens*. Yunnan, *Rock 5164* (US).

Figure 7. *Sinosidus argyropholis*. Holotype (UPS).

Figure 8. *Sinosidus argyropholis*. Sichuan. Holotype (PE) of *Aster argyropholis* var. *niveus*.

Figure 9. *Sinosidus argyropholis*. Sichuan. *Li Xin 75124* (PE).

Figure 10. *Sinosidus argyropholis*. Sichuan. *Zhao Qingsheng 1569* (PE).

Figure 11. *Sinosidus argyropholis*. Sichuan. *Wang 21336* (PE).

Figure 12. *Sinosidus paradoxus*. Sichuan. Holotype (PE) of *Aster argyropholis* var. *paradoxus*.

Figure 13. *Sinosidus paradoxus*. Sichuan. Isotype (KUN) of *Aster argyropholis* var. *paradoxus*.

Figure 14. *Sinosidus fulgidulus*. Tibet. Holotype (E).

Figure 15. *Sinosidus hypoleucus*. Tibet. Holotype (BM).

Figure 16. *Sinosidus lavandulifolius*. Sichuan. Isolectotype (US).

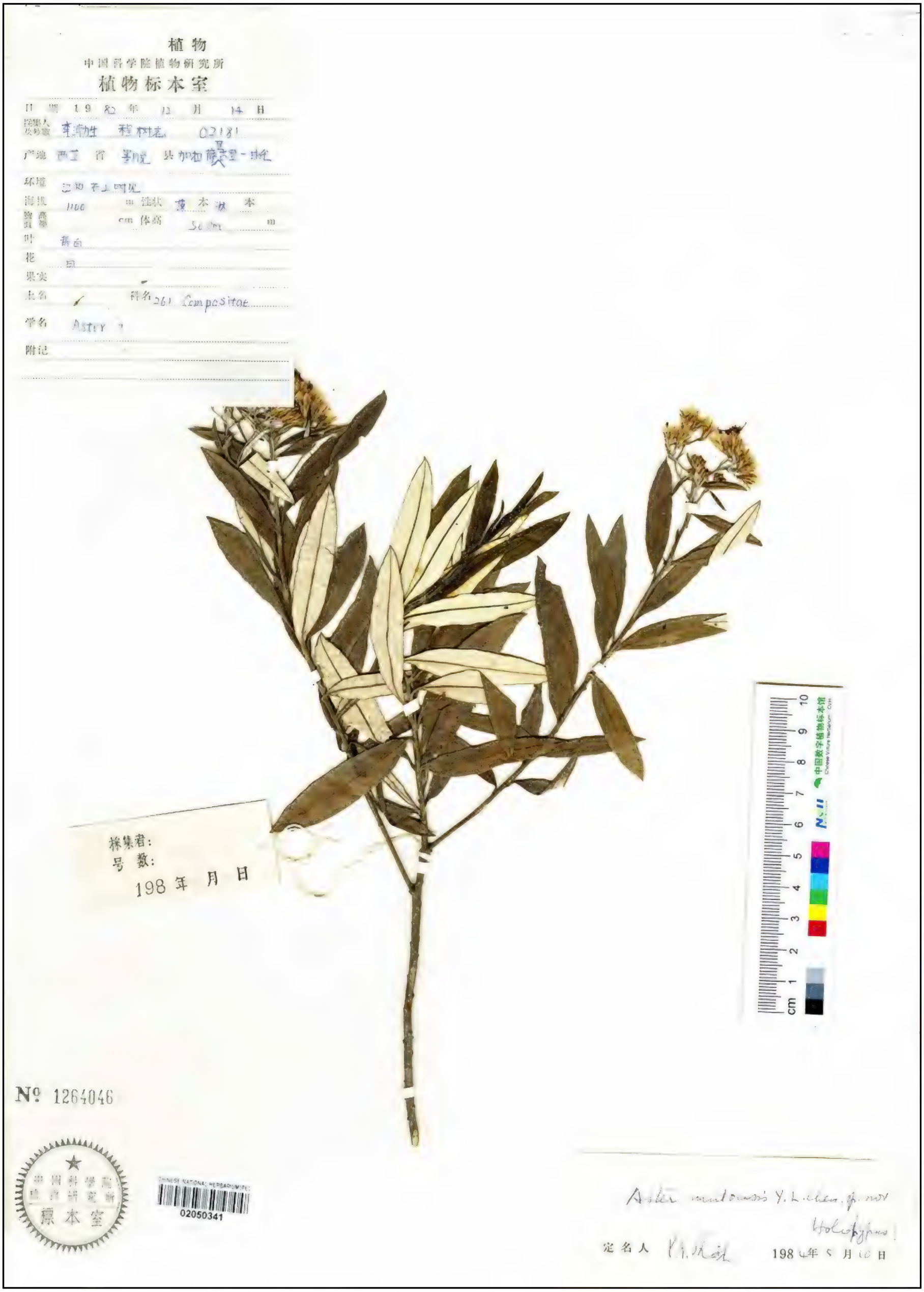

Figure 17. *Sinosidus motuoensis*. Tibet. Holotype (PE).

Figure 18. *Sinosidus polius*. Sichuan. Isotype (US).

GRIERSONIA Nesom, **gen. nov. TYPE:** *Griersonia fuscescens* (Bureau & Franchet) Nesom

Perennial herbs from fibrous-rooted rhizomes; stems, leaves, peduncles, and phyllaries prominently stipitate-glandular, hirsutulous to hirsute or hispidulous-hirsute. **Stems** 15–60 cm. **Leaves** basal and cauline or basal withering by flowering, cauline (basal withered) or mostly basal (cauline reduced in size), blades ovate to elliptic, base rounded or truncate to attenuate, margins shallowly serrate. **Capitula** in dense (*G. fuscescens*) to loose (*G. oblongifolia*, *G. senecioides*) corymbs, peduncles from a region of foreshortened internodes. **Involucres** hemispheric to campanulate, 12–14 cm wide (pressed); phyllaries in 3(–4) equal to subequal series, linear-lanceolate to oblanceolate-oblong, outer green at least distally, inner scarious, apex acute. **Ray florets** 15–25, tube 2–3.5 mm long, ligules purplish to bluish, not reflexing or coiling. **Disk florets** 5–7.5 mm long, lobes ovate to triangular, spreading, sometimes tip recurved. **Achenes** narrowly obovate to oblanceolate, compressed, 3–3.5 mm long, 2–4-nerved (2 lateral nerves and one on each face), strigose, sessile-glandular; pappus 3–4-seriate, longest bristles as long as the disc corollas, clavate-tipped, outer bristles 0.5–1.2 mm long.

The genus is named for A.J.C. Grierson (1929-1990), specialist in Asteraceae at the Royal Botanic Garden Edinburgh from 1951 until his death (see Hedge & Long 1994). He published a revision of *Psychrogeton* and contributed treatments of many genera of Asteraceae for the Flora of Turkey. He was author in 1980 of Compositae in the Revised Handbook to the Flora of Ceylon, made contributions in 1982 to Flora Iranica, and was a major contributor to the the Flora of Bhutan. His study of Himalyayan asters provides baseline information for study of the genus.

1. Leaves cauline (basal withered), blades broadly ovate, base truncate to a narrow petiole; heads 7–35 ..... **Griersonia fuscescens**
1. Leaves mostly basal, cauline reduced in size distally, blades elliptic to elliptic-oblanceolate or elliptic-lanceolate, base attenuate to a petiole or petiolar region or epetiolate; heads 3–12.
   2. Basal leaves with sharply delimited petioles; phyllaries linear-lanceolate ..... **Griersonia oblongifolia**
   2. Basal leaves attenuate to petiolar region; phyllaries oblong-oblanceolate ..... **Griersonia senecioides**

1. Griersonia fuscescens (Bureau & Franchet) Nesom, **comb. nov.** *Aster fuscescens* Bureau & Franchet, J. Bot. (Morot). 5: 49. 1891. **TYPE**: **CHINA**. **Sichuan**. Se-tchuen, environs de Ta-tsien-lou, [1896?], *Prince H. d'Orléans s.n.* (holotype: P image).

Aster doronicifolius H. Lév., Repert. Spec. Nov. Regni Veg. 12: 283. 1913. **TYPE**: **CHINA**. **Yunnan**. "Pâturages du haut plateau de Ta-Hai, 3200 m," Jul 1902, *E.E. Maire s.n.* (holotype: E image, Fig. 4).

Sichuan, Yunnan; 2700–4200 m.

Grierson (1964), followed by Ling (1985) and Chen et al. (2011), included *Aster fuscescens* var. *scaberoides* as part of the species. Especially in phyllary morphology, however, this entity (species) does not appear to belong with the *Griersonia* taxa. Nor does it appear to fit within *Cordiofontis* or *Cardiagyris*, which have cordate-leaved species. Var. *scaberoides* is a distinct entity known from a number of collections in Yunnan.

Aster fuscescens var. *scaberoides* C.C. Chang, Bull. Fan Mem. Inst. Biol., Bot. 6: 46. 1935. **TYPE**: **CHINA**. **Xizang**. SE Tibet, Tsarong, open alpine meadows on the Salwin-Kiu Chiang divide, NW of Si-chi-to, 28° 48'N, 98° 15' E, 14,000 ft, Oct 1922, *G. Forrest 22823* (holotype: K image).

2. Griersonia oblongifolia (Grierson) Nesom, **comb. nov.** *Aster fuscescens* var. *oblongifolius* Grierson, Notes Roy. Bot. Gard. Edinburgh. 26: 93. 1964. **TYPE**: **MYANMAR**. Upper Burma, neighborhood of forest region N of Tahawndam, Upper Adung Valley, on meadow clad scree chutes and in gullies in the forest belt where Picea and Larch appear, 10,000-11,000 ft, 27 Sep 1931, *F. Kingdon-Ward 10127* (holotype: BM, Fig. 7).

Griersonia oblongifolia apparently is known only from two collections, both made by Kingdon-Ward in September 1931. The type is from close to the Tibetan border; the other is from a closely adjacent locality at the border: **CHINA**. **Xizang**: Tibetan side of Namni La Pass, 28° 35' N, 98° E, 3350 m, 3 Sep 1931, *Kingdon-Ward 10025* (BM, as cited by Grierson). Chen et al. (2011) described the geographic distribution based on the two collections cited by Grierson. 3050–3350 m.

3. Griersonia senecioides (Franch.) Nesom, **comb. nov.** *Aster senecioides* Franch., J. Bot. (Morot). 10: 381. 1896. **TYPE**: **CHINA**. **Yunnan**. Collines ombragées au dessus de Ta-pin-tze, 7 Sep 1882, *R.P. Delavay 606* (holotype: P 00711751 image, Fig. 8, typification as indicated by P annotation; isotypes: P-3 sheets images).

Aster senecioides var. *latisquamus* Y. Ling, Fl. Reipubl. Popularis Sin. 74: 360, 252. 1985. **TYPE**: **CHINA**. **Yunnan**. Heqing Xian, Jiangyig, in the forest, 14 Sep 1929, *R.C. Ching 24629* (holotype: PE image).

Southwest Sichuan, north and northwest Yunnan; 2000–3000 m.

Chen et al. (2011) noted that "Two varieties of *Aster senecioides* have been recognized. However, upon examination of specimens, the width of the scarious phyllary margin is identical, and phyllary width and ray floret lamina width overlap significantly."

Figure 1. *Griersonia fuscescens* involucres.

Figure 2. *Griersonia* involucres. Top: *G. oblongifolia* (BM holotype). Bottom: *G. senecioides* (P isotype).

Figure 3. *Griersonia fuscescens*. Yunnan. Cultivated at Edinburgh (E).

Figure 4. *Griersonia fuscescens*. Yunnan. Holotype of *Aster doronicifolius* (E).

Figure 5. *Griersonia fuscescens*. Yunnan. *Rock 9716* (US).

Figure 6. *Griersonia fuscescens.* Yunnan, *Rock 17272* (US).

Figure 7. *Griersonia oblongifolia*. Holotype, BM.

Figure 8. *Griersonia senecioides*. Yunnan. Holotype of *Aster senecioides* (P).

Figure 9. *Griersonia senecioides*. Sichuan. *Rock 18329* (US).

Figure 10. *Griersonia senecioides.* Sichuan. *Boufford et al. 42847* (P).

Figure 11. *Griersonia senecioides.* Yunnan. *1984 Sino-Amer. Bot. Expedition 1467* (US). Showing tendency for peduncles to arise from a region of foreshortened internodes, characteristic of the genus.

Figure 12. *Griersonia senecioides*. Sichuan. A plant from the collection locality of *Bouffourd et al. 42847* of Figure 10.

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NEW GENERA FROM AUSTRALIAN *OLEARIA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Ten new genera, including 29 species, are recognized from among species previously identified within Australian *Olearia*.

Landerolaria Nesom, **gen. nov.** — **L. arckaringensis** (P.J. Lang) Nesom, comb. nov., **L. eremaea** (Lander) Nesom, comb. nov., **L. gordonii** (Lander) Nesom, comb. nov., **L. humilis** (Lander) Nesom, comb. nov., **L. laciniifolia** (Lander) Nesom, comb. nov., **L. macdonnellensis** (D.A. Cooke) Nesom, comb. nov., **L. newbeyi** (Lander) Nesom, comb. nov., **L. orientalis** (A.R. Bean & Jobson) Nesom, comb. nov., **L. stuartii** (F. Muell.) Nesom, comb. nov., **L. xerophila** (F. Muell.) Nesom, comb. nov.

Neolaria Nesom, **gen. nov.** — **N. bella** (A.R. Bean & Jobson) Nesom, comb. nov., **N. ferresii** (F. Muell.) Nesom, comb. nov., **N. mucronata** (Lander) Nesom, comb. nov.

Phaseolaria Nesom, **gen. nov.** — **P. elliptica** (DC.) Nesom, comb. nov., **P. fulgens** (A.R. Bean) Nesom, comb. nov., **P. praetermissa** (P.S. Green) Nesom, comb. nov.

Walsholaria Nesom, **gen. nov.** — **W. calcarea** (F. Muell. ex Benth.) Nesom, comb. nov., **W. cuneifolia** (Bean & Mathieson) Nesom, comb. nov., **W. magniflora** (F. Muell.) Nesom, comb. nov., **W. muelleri** (Sond.) Nesom, comb. nov.

Muellerolaria Nesom, **gen. nov.** — **M. rudis** (Benth.) Nesom, comb. nov., **M. picridifolia** (F. Muell.) Nesom, comb. nov.

Vicinia Nesom, **gen. nov.** — **V. ciliata** (Benth.) Nesom, comb. nov., **V. squamifolia** (F. Muell.) Nesom, comb. nov.

Wollemiaster Nesom, **gen. nov.**— **W. cordatus** (Lander) Nesom, comb. nov.

Eoglandula Nesom, **gen. nov.** — **E. glandulosa** (Labill.) Nesom, comb. nov., **E. suffruticosa** (D.A. Cooke) Nesom, comb. nov.

Linealia Nesom, **gen. nov.** — **L. floctoniae** (Maiden & Betche) Nesom, comb. nov.

Ephedrides Nesom, **gen. nov.**—**E. trifurcata** (Lander) Nesom, comb. nov.

A description for each genus is provided and the species are illustrated. Formal typification is provided for each species. Lectotypes are designated for *Aster huegelii* var. *squamifolius*, *Eurybia ciliata*, *Olearia picridifolia*, and *O. rudis*.

Cross et al. (2002) showed that Australasian *Olearia* is polyphyletic, based on ITS sequence data. *Olearia* species from New Zealand, New Guinea, and some from Tasmania, Lord Howe Island, and mainland Australia are distantly related to most of the Australian ones, including the generic type *O. tomentosa* (Cross et al. 2002; Wagstaff et al. 2011; Saldivia et al. 2020) and are placed in a different subtribe (subtr. Celmisiinae; Saldivia in Nesom 2020).

Many of the Australian species placed by Bentham (1867) in sect. *Adenotriche* (glabrous vestiture) are positioned by molecular data (Cross et al. 2002; Brouillet et al. 2009) among other accepted Australian genera, while others (*O. hookeri*, *O. imbricata*, *O. passerinoides*, *O. teretifolia*) are related or closely similar in morphology to sect. *Eriotriche*, which in turn is directly related to *Olearia* in a stricter sense (see below).

Species of sects. *Eriotriche*, *Asterotriche*, and sect. *Dicerotriche* sensu stricto (*Olearia tomentosa*) form a strongly supported clade ("clade A" of Cross et al.). Australian sect. *Asterotriche* is monophyletic (Messina et al. 2013, 2014); the status of *O. tomentosa* is unsettled (see Saldivia et al.

2020 and comments under subtribe Celmisiinae by Saldivia in Nesom 2020). Sect. *Eriotriche* is not monophyletic, if by definition it includes all species with 'wool-producing hairs' (see Lander 1990 for illustrations), but these species as a group still are evolutionarily distinct from the sect. *Asterotriche* /*O. tomentosa* clade. The newly segregated *Landerolaria*, *Vicinia*, and *Wollemiaster* produce "Eriotriche" hairs — if these latter genera are accepted, segregation of sect. *Eriotriche* species at generic rank also is justified. Admixtures of glandular and eglandular hairs have made characterization of sect. *Merismotriche* problematic, and some species of the sect. *Eriotriche* alliance appear to have completely lost hairs, becoming glabrous.

Subgroups can be discerned within "clade A" *Eriotriche*. The mophological consistency of these groups needs to be confirmed and it remains to be seen whether they are evolutionarily discrete — this whole "clade A" *Eriotriche* aggregate might be treated as a single genus or segregates might be recognized.

* the O. ramulosa group: *O. adpressa?, O. algida, O. ericoides, O. ramosissima, O. ramulosa*. *Olearia ramosissima* and *O. ramulosa* are included as molecular samples within "clade A" sect. *Eriotriche* of Cross et al. (2002).
* the O. exiguifolia group: *O. exiguifolia*. Not included in molecular analyses.
* the O. microphylla group: *O. brachyphylla, O. lanuginosa, O. lepidophylla, O. microphylla*. *Olearia microphylla* is included as a molecular sample within sect. *Eriotriche* of clade A of Cross et al. (2002).
* the O. axillaris group: *O. arida*, *O. axillaris*, *O. revoluta*. None included in molecular analyses.
* the O. glutinosa group: *O. cassiniae, O. decurrens, O. glutinosa, O. microdisca, O. plucheacea, O. racemosa, O. subspicata, O. tubuliflora*. *Olearia decurrens* and *O. plucheacea* are unusual in producing toothed leaves and perhaps are sister species. The ebracteate peduncles of *O. plucheacea* are unusual. None included in molecular analyses.
* the O. pimeleoides group: *O. burgessii, O. fluvialis, O. incana, O. incondita, O. iodochroa, O. minor, O. occidentissima, O. pimeleoides, O. propinqua*. *Olearia pimeleoides* is included as a molecular sample within sect. *Eriotriche* of clade A of Cross et al. (2002).
* the O. tenuifolia group: *O. adenolasia**, *O. adenophora**, *O. ballii, O. curticoma, O. elaeophila, O. floribunda?**, *O. homolepis**, *O. hookeri, O. imbricata, O. lehmanniana, O. muricata**, *O. passerinoides, O. paucidentata**, *O. stricta**, *O. strigosa, O. tenuifolia**, and *O. teretifolia* Western Australia endemics *O. elaeophila*, *O. lehmaniana*, *O. muricata*, *O. paucidentata*, and *O. strigosa* were studied as a group by Lander (2008a). Species with an asterisk are hirsute to hispid. Walsh (2014) regarded *O. adenophora* as a synonym of variable *O. tenuifolia*. *Olearia ballii*, *O. floribunda*, and *O. passerinoides* are included as molecular samples within sect. *Eriotriche* of clade A of Cross et al. (2002).

Some species of Bentham's sect. *Merismotriche* are segregated here as distinct genera (*Landerolaria, Neolaria, Muellerolaria*, *Vicinia*). Others (*O. adenophora*, *O. floribunda*, O. *homolepis*, *O. muricata*, *O. paucidentata*, *O. stricta*, *O. strigosa*, *O. tenuifolia*) are placed here in the *O. tenuifolia* group of "clade A Eriotriche."

In any case, little is gained by continuing to identify species as *Olearia* when they are outside the bounds, morphologically and molecularly, of *Olearia* (sensu clade A of Cross et al.) and more closely related to other accepted genera of Brachyscominae. Some of the species moved here to new genera have not been included in molecular sampling but are considered in context of their morphology.

Placement of *Olearia arguta* Benth. as closely related to *Camptacra* (Lowrey et al. 2001; Cross et al. 2002) has resulted from confusion regarding its identity — the Cross et al. molecular sample (from Queensland) apparently is identified by Bean (2020) as *Camptacra robusta* Bean. The type of *O. arguta* (*R. Brown 2253*, probable holotype: BM image; probable isotypes: MEL image, P image; not included in Bean's revision) belongs with *Camptacra* — based on its geography, it presumably would be identified by Bean as *C. gracilis*, but its morphology seems out of place in that species.

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Thanks to Julia Percy-Bower and staff at PERTH for sending an image of *Olearia fluvialis* , Andrew Franks at BRI for sending an image of the *Olearia bella* holotype, and to Patricio Saldivia for a very helpful review.

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LANDEROLARIA Nesom, **gen. nov.** **TYPE**: *Landerolaria stuartii* (F. Muell.) Nesom

Aromatic shrubs usually with a mixture of biseriate glandular hairs and two types of uniseriate, eglandular hairs; leaves oblong to narrowly lanceolate or elliptic, epetiolate, margins regularly toothed; heads solitary or in loose terminal clusters on few-bracteate peduncles; achenes densely sericeous. For Australian botanist Nicholas S. Lander.

Shrubs, often aromatic, taprooted (as described for *Olearia arckaringensis*). **Stems** to 0.3-2 m, with stipitate-glandular hairs or a mixture of biseriate glandular hairs and uniseriate, eglandular hairs. or eglandular, often resinous. **Leaves** alternate, narrowly oblong to narrowly lanceolate, obovate, or elliptic, attenuate-epetiolate (petiolate in *L. macdonnellensis* and *L. xerophila*), 0.2–0.3 (in *L. humilis*) or 1–11.5 cm long, margins serrate to crenate with 2–8(–15 in *L. laciniifolia*) pairs of teeth, with sessile glands to minutely stipitate-glandular, glabrescent, often resinous. **Heads** 1 or few in loose clusters; peduncles minutely bracteate, 1–8 cm long; receptacles shallowly convex, weakly alveolate. **Involucres** broadly campanulate; phyllaries 3–5-seriate, graduate in length, linear-elliptic, longest 3.5–4.5 mm long, sessile glandular or eglandular. **Ray flowers** 8–64, ligules 5–15 mm long, white to blue, purple, or mauve, coiling at maturity. **Disc flowers** bisexual, fertile, corollas narrowly cylindric, 4–9 mm long, the tube barely expanded into the limb. **Achenes** narrowly obovoid, 1.8–4 mm long, compressed, numerous-nerved, sparsely strigose (*L. orientalis*) to densely sericeous, sometimes also glandular; pappus 1- or 2-seriate, bristles 20–55, 4–8 mm long.

In the molecular-phylogenetic analysis of Cross et al. (2002), a strict consensus tree places *Olearia stuartii* in an unresolved position among taxa of Brachyscominae. Another consensus tree (their Fig. 3, with reduction of taxa in Celmisiinae) places it with *O. ferresii* as a weakly supported supported pair within the Brachyscominae as sister to *Tetramolopium vagans*, outside the bounds of a more strictly defined *Olearia*. *Tetramolopium vagans* (Pedley 1993) seems morphologically in place within *Tetramolopium*, although the epithet is meant to reflect its geographic displacement from close related congeners and molecular data (Lowrey et al. 2001) indicate that it is not closely related to the rest of the genus. *Olearia ferresii* is distinct in morphology from the *Landerolaria* species and treated here as a member of the genus *Neolaria*.

Lander (1989) noted that *Olearia gordonii*, *O. humilis*, *O. stuartii*, and *O. xerophila* comprise a "natural group with no other close relatives." Species newly described since then (*O. arckaringensis*, *O. eremaea*, *O. laciniifolia*, *O. newbeyi*, and *O. orientalis*) appear to belong with the first four, as does *O. macdonnellensis* (described in 1986). The additions considerably increase the morphological diversity of the group, and it would not be surprising to find that more than a single clade is represented.

As alluded to by Lander (1990), *Olearia laciniifolia* is similar to *O. rudis* (see the genus *Muellerolaria*, this publication) in its hirsute vestiture of long, uniseriate, multicellular hairs —but *O. xerophila* (of *Landerolaria*) also is hirsute. *Olearia laciniifolia* differs from *O. rudis* in its fully shrubby habit, abundant glandular hairs, 4–5-seriate phyllaries graduate in length, and strigose-sericeous achenes. *Olearia arckaringensis* is unusual in *Landerolaria* in the density of its lanate vestiture.

Olearia tridens (Cooke 1986), from Northern Territory, is at least superficially similar to *O. stuartii* and the two were compared in the protologue of the latter, but Lander (1987) transferred *O. tridens* to *Minuria*.

1. Heads in loose corymbs.
   2. Leaves 2–12 mm long ..... **Landerolaria newbeyi**
   2. Leaves 10–75 mm long.
      3. Leaves broadly elliptic-obovate ..... **Landerolaria macdonnellensis**
      3. Leaves linear to narrowly oblong ..... **Landerolaria gordonii**

1. Heads solitary on bracteate peduncles
   4. Heads terminal and on axillary branches in a diffuse (paniculate) array ..... **Landerolaria humilis**
   4. Heads on bracteate peduncles, solitary or loosely clustered above the leaves.
      5. Stems and leaves hirsute-villous .....**Landerolaria laciniifolia**
      5. Stems and leaves lanate or minutely pubescent to glabrescent or subglabrous.
         6. Leaves oblong to oblanceolate or linear-oblanceolate ..... **Landerolaria stuartii**
         6. Leaves elliptic to elliptic-obovate.
            7. Stems closely white-lanate, vestiture obscuring the stem surface .. **Landerolaria arckaringensis**
            7. Stems glandular and hairy, vestiture not obscuring the stem surface.
               8. Peduncles mostly obscured by closely spaced, ascending leaves ..... **Landerolaria eremaea**
               8. Peduncles visible above distal leaves
                  9. Leaves hirsute and glandular, margins serrate with 7–9 pairs of sharp teeth ..... **Landerolaria xerophila**
                  9. Leaves resinous but glabrous, margins crenate-dentate with 1–3 pairs of low teeth ..... **Landerolaria orientalis**

1. Landerolaria gordonii (Lander) Nesom, **comb. nov.** *Olearia gordonii* Lander, Nuytsia 7: 32. 1989. **TYPE**: **Queensland**. On the very dry slopes of the Bendee ridges between Glenmorgan and Surat, and on the Thomby Range, with *Acacia catenulata*, no date, *D.M. Gordon 80* (holotype: BRI; isotype: PERTH, Fig. 1).

Queensland. Flowering (May)June–September(–October).

2. Landerolaria newbeyi (Lander) Nesom, **comb. nov.** *Olearia newbeyi* Lander, Nuytsia 18: 100. 2008. **Type**: **Western Australia**. 17 km NNE of Peak Charles, ca. 78 km SE of Norseman, scattered in patches in *Thryptomene australis* High Shrubland (disturbed roadside), 21 Jan 1985, *K.R. Newbey 10897* (holotype: PERTH 06105424 image; isotypes: PERTH-2 sheets images, Fig. 2).

Western Australia. Flowering August–January.

3. Landerolaria humilis (Lander) Nesom, **comb. nov.** *Olearia humilis* Lander, Nuytsia 7: 26. 1989. **TYPE**: **Western Australia**. Sandstone to Yuinmery Road, 3 km S of turnoff to Atley Homestead [on Sandstone-Paynes Find road], 28° 15 S, 119° 05' E, compact sandy loam, tall open shrubland with *Acacia* dominant, 25 Aug 1986, *P.S. Short 2563* - voucher for chrom. no. det. of n = 9 (holotype: PERTH image; isotypes: K-2 sheets images, MEL-2 sheets images, Fig. 3).

Western Australia. Flowering (June–)July–October.

4. Landerolaria stuartii (F. Muell.) Nesom, **comb. nov.** *Eurybia stuartii* F. Muell., Fragm. Phyt. Aust. 1: 202. 1859. *Aster stuartii* (F. Muell.) F. Muell., Fragm. Phyt. Aust. 5: 76. 1865. *Olearia stuartii* (F. Muell.) Benth., Fl. Austral. 3: 481. 1867. **TYPE**: **South Australia**. NW interior of

South Australia, [1859], *J.M. Stuart s.n.* (holotype: MEL image; isotype: K image). Protologue: "In regionibus interioribus boreali-occidentalibus coloniae South Australia."

Aster megalodontus F. Muell., Fragm. Phyt. Aust. 8: 244. 1874. **TYPE**: **Northern Territory**. Protologue: "In monte Olgae; E. Giles." Not seen; as synonym of *Olearia stuartii* fide Electronic Flora of South Australia database.

Northern Territory, South Australia, Western Australia. Flowering June–September.

5. Landerolaria laciniifolia (Lander) Nesom, **comb. nov.** *Olearia laciniifolia* Lander, Nuytsia 72: 149. 1990. **TYPE**: **Western Australia**. Newdegate-Lake Grace road, 22 Sep 1964, *A.R. Fairall 1623* (holotype: PERTH image, Figs. 10, 11; isotype: KPBG).

Western Australia. Flowering June–November.

6. Landerolaria eremaea (Lander) Nesom, **comb. nov.** *Olearia eremaea* Lander, Nuytsia 72: 141. 1990. **TYPE**: **Western Australia**. Beegul [Rockhole], 93 mi NE of Cosmo Newberry, above breakaway, 25 Aug 1961, *A.S. George 2881* (holotype: PERTH image, Fig. 7).

Western Australia. Flowering July–August.

7. Landerolaria arckaringensis (P.J. Lang) Nesom, **comb. nov.** *Olearia arckaringensis* P.J. Lang, J. Adelaide Bot. Gard. 22: 57. 2008. **TYPE**: **South Australia**. Region 2: Lake Eyre, Arckaringa Station, breakaway slopes facing Arckaringa Creek, on the scree slopes, below the crest, well out of the creek bed proper, with *Senna*, *Stackhousia*, *Ptilotus*, *Lotus*, *Goodenia*, *Acacia*, *Gunniopsis*, *Aristida*, *Scaevola*, 28 Jun 2000, *D.E. Symon 16109* (holotype: AD image: isotypes: AD image, K-2 sheets images Fig. 8, NT image, PERTH image).

South Australia. Flowering (March–)May–September.

8. Landerolaria xerophylla (F. Muell.) Nesom, **comb. nov.** *Eurybia xerophylla* F. Muell., Fragm. Phyt. Aust. 1(3): 51. 1858. *Aster xerophyllus* (F. Muell) F. Muell., Fragm. Phyt. Aust. 5(35): 76. 1865. *Olearia xerophylla* (F. Muell.) Benth., Fl. Austr. 3. 486. 1867. **LECTOTYPE** (designated here): **Queensland**. Barren ridges, upper Burdekin, no date, *F. Mueller s.n.* (K 838941 image, lower row of stems). Protologue: "In collibus sterilioribus ad fluvium Burdekin." MEL 1547184 image (lower left stem) is a possible isolectotype, but the label has "Range between the Flinders and Burdekin R."

Aster heynei F. Muell., Fragm. Phyt. Aust. 5(35): 86. 1865. **LECTOTYPE** (designated here): **Queensland**. Cape River, no date, *E.M. Bowman 221* (MEL 1547108 image-upper 2 plants; possible isolectotype: K 838941 image, upper plant). Protologue: "Ad flumen Cape's River. Bowman."

Queensland, Western Australia. Flowering mostly May–September but continuing sporadically all year. Lander (1989) noted that the wide disjunction suggests that the species once had a wider distribution. Figure 6.

9. Landerolaria macdonnellensis (D.A. Cooke) Nesom, **comb. nov.** *Olearia macdonnellensis* D.A. Cooke, Muelleria 6: 181. 1986. **TYPE**: **Northern Territory**. 1 km W of Ellery Creek Big Hole, 23° 47′ S, 133° 03′ E, 17 Jul 1983, *P.K. Latz 9636* (holotype: NT not seen; isotypes: CANB-2 sheets images, DNA image-Fig. 4, NT).

Northern Territory. Flowering August–September.

10. Landerolaria orientalis (A.R. Bean & Jobson) Nesom, **comb. nov.** *Olearia orientalis* A.R. Bean & Jobson, Austrobaileya 10: 106. 2017. **TYPE**: **Queensland**. Port Curtis District, 3 km E of Glenavon homestead, Five Mile Creek headwaters, 1 Mar 1994, *P.I. Forster PIF15039* (holotype: BRI [2 sheets]; isotypes: AD, CANB, DNA, K, L, MEL, NSW, PE). No types seen.

Figure 1. *Landerolaria gordonii*. Queensland. Isotype (PERTH).

Figure 2. *Landerolaria newbeyi*. Western Australia. Isotype (PERTH).

Figure 3. *Landerolaria humilis*. Isotype (MEL).

Figure 4. *Landerolaria macdonnellensis*. Isotype (DNA).

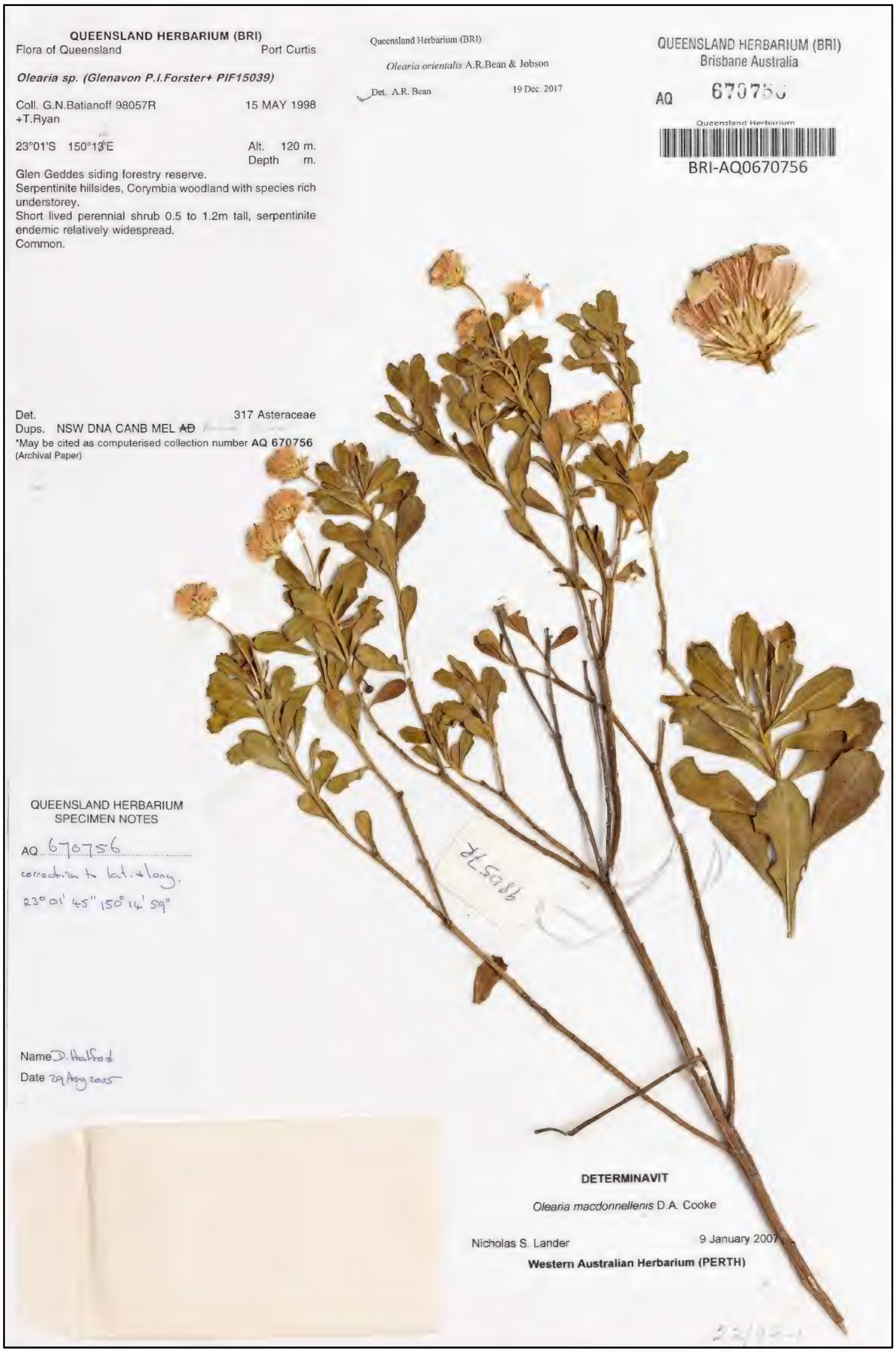

Figure 5. *Landerolaria orientalis*. Queensland. *Batianoff 98057R* (BRI).

Figure 6. *Landerolaria xerophila*. Queensland. *White 123361* (US).

Figure 7. *Landerolaria eremaea*. Western Australia. Holotype of *Olearia eremaea* (PERTH).

Figure 8. *Landerolaria arckaringensis*. South Australia. Isotype (K).

Figure 9. *Landerolaria stuartii*. Northern Territory. *Lazarides 5950* (US).

Figure 10. *Landerolaria laciniifolia*. Western Australia. Holotype of *Olearia laciniifolia* (PERTH).

Figure 11. *Landerolaria laciniifolia*. Details from holotype.

NEOLARIA Nesom, **gen. nov.** **TYPE**: *Neolaria ferresii* (F. Muell.) Nesom

Distinct in its elongate, thickened, epetiolate leaves with entire to mucronulate or serrulate margins, linear-bracteate peduncles, heads terminal and from distal nodes in a loosely corymboid cluster, and densely sericeous achenes.

Shrubs, aromatic. **Stems** 50–150 cm, spreading eglandular hairs (multicellular, uniseriate) and sparsely stipitate-glandular (multicellular, biseriate) to glabrescent or glabrous; oil glands sometimes present on ribs. **Leaves** alternate, linear to lanceolate to oblong-lanceolate, epetiolate, 1.5–11.5 cm long, thickened, margins entire to mucronulate, denticulate, or serrulate, teeth sometimes mostly distal, minutely hirsute, sessile- or minutely stipitate-glandular. **Heads** terminal and from distal nodes, appearing as a loose corymboid cluster; peduncles 1–7 cm long, with linear to linear-lanceolate bracts. **Involucres** campanulate; phyllaries 4–5-seriate, graduate in length, longest 5–11 mm, linear to linear-lanceolate, sessile-glandular; receptacles alveolate. **Ray flowers** 8–18, ligules 9–16 mm long, white to mauve or purple, coiling at maturity. **Disc flowers** bisexual, fertile, corollas yellow, 7–9 mm long, lobes triangular, reflexing. **Achenes** narrowly obovoid, compressed, 3–4 mm long, 3-ribbed, densely sericeous, eglandular; pappus 1- or 2-seriate, bristles 24–40, 7–9 mm long, apically expanded, sometimes with a shorter outer series.

In the molecular-phylogenetic analysis of Cross et al. (2002), a strict consensus tree places *Olearia ferresii* in an unresolved position among taxa of Brachyscominae. Another consensus tree (their Fig. 3, with reduction of taxa in Celmisiinae) places it with *O. stuartii* as a weakly supported pair within the Brachyscominae. The three species segregated here as *Neolaria* appear distinct as a group and disconnected from *O. stuartii* and its relatives (see *Landerolaria*).

Lander (1990) noted that ray corollas of *Landerolaria ferresii* and *L. mucronata* produce druse crystals not seen elsewhere in *Olearia* sensu lato except in *O. incana* (of the *O. pimeleoides* group of "clade A" sect. *Eriotriche*).

1. Leaves linear-lanceolate, 1–5 mm wide, margins entire to mucronulate with a few teeth ..... **Neolaria mucronata**
1. Leaves mostly lanceolate to oblong-lanceolate, 6–22 mm wide, margins shallowly serrate to serrate-mucronate or denticulate with 15–20 pairs of evenly and closely spaced teeth.

2. Stems and leaves with mostly glandular hairs, rarely with minute eglandular hairs; oil glands present on stems and leaves; veins of decurrent leaf base not forming stem ribs; rays 8–10, ligules cream to white ..... **Neolaria ferresii**
2. Stems and leaves densely and evenly hirsutulous, with only eglandular hairs; oil glands absent from stems and leaves; veins of decurrent leaf base continuing onto the stem and forming ribs; rays 14–18, ligules mauve to purple ..... **Neolaria bella**

1. Neolaria ferresii (F. Muell.) Nesom, **comb. nov.** *Eurybia ferresii* F. Muell., Fragm. Phyt. Aust. 3: 18, t. 18. 1862. *Aster ferresii* (F. Muell.) F. Muell., Fragm. Phyt. Aust. 5: 75. 1865. *Olearia ferresii* F. Muell. ex Benth., Fl. Aust. 3: 487. 1867. **TYPE**: **Northern Territory**. Brinkley's Bluff, Macdonnell Ranges, [1859], *J.M. Stuart s.n.* (holotype: MEL image, Fig. 4).

Northern Territory, South Australia, Western Australia. Flowering May–October.

2. Neolaria bella (A.R. Bean & Jobson) Nesom, **comb. nov.** *Olearia bella* A.R. Bean & Jobson, Austrobaileya 10: 102. 2017. **TYPE**: **Queensland**. Warrego District: ca. 15 km S of Quilpie, towards Eulo, S-facing slope of mesa, with *Acacia* open woodland, gravelly, eroded Ferricrete duricrust, locally occasional shrub 1.25 m high, 4 Sep 1990, *P.G. Wilson 513* (holotype: BRI, Fig. 2; isotypes: NSW, PERTH, not seen).

Queensland. Flowering June–September.

3. Neolaria mucronata (Lander) Nesom, **comb. nov.** *Olearia mucronata* Lander, Nuytsia 72: 151. 1990. **TYPE**: **Western Australia**. Wittenoom, Jan 1972, *McGuire 18* (holotype: PERTH image, Fig. 1).

Western Australia. Flowering July–November(–January).

Figure 1. *Landerolaria mucronata*. Western Australia. Holotype of *Olearia mucronata* (PERTH). Arrow points to leaf with mucronate margins.

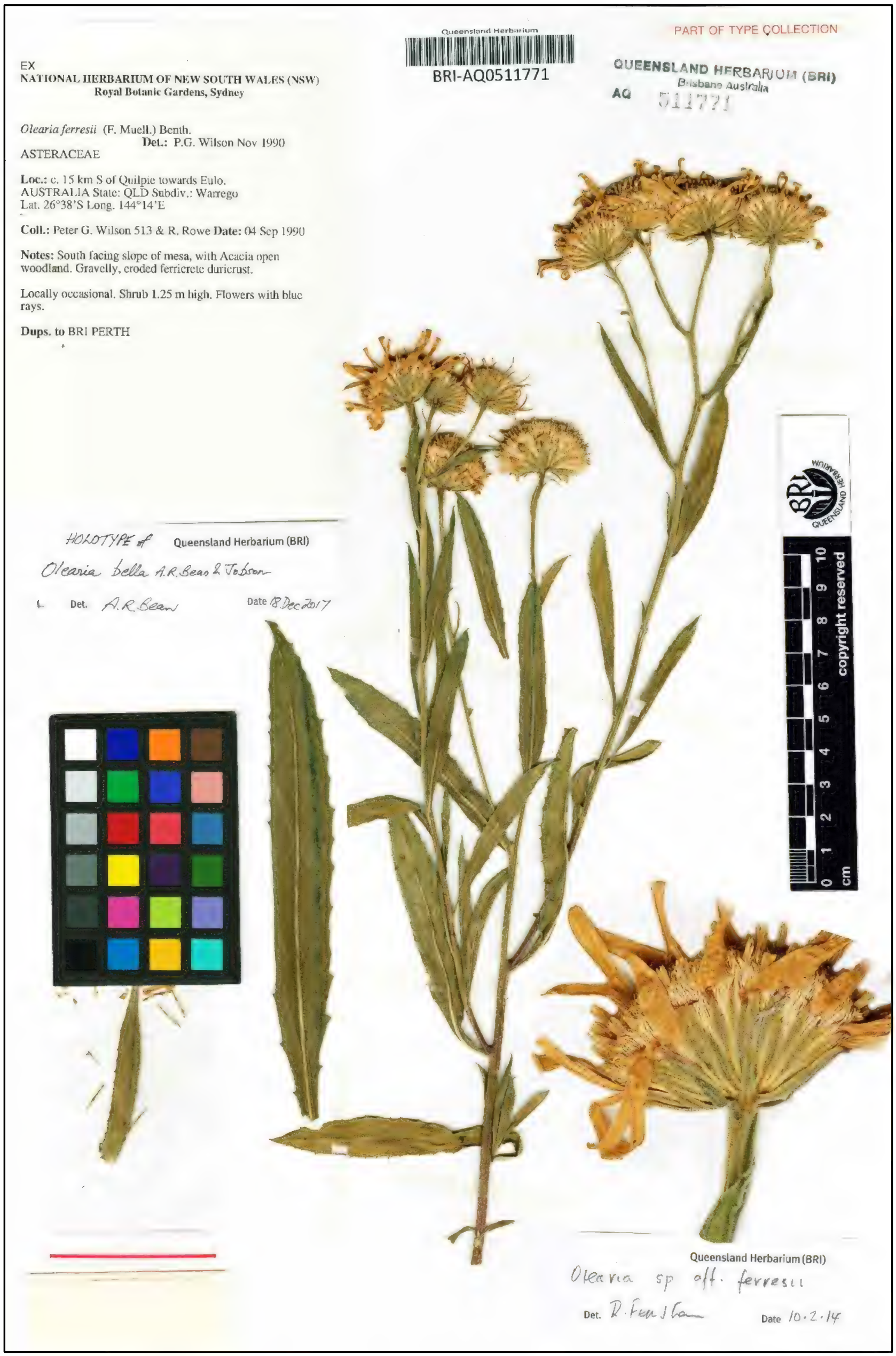

Figure 3. *Landerolaria bella*. Holotype (BRI).

Figure 3. *Landerolaria ferresii*. Northern Territory. *Lazarides 6158* (US).

Figure 4. *Landerolaria ferresii*. Holotype (MEL).

Figure 5. *Landerolaria ferresii*. South Australia. Seeds of South Australia, Conservation Center.

Figure 6. *Landerolaria ferresii*. South Australia. Seeds of South Australia, Conservation Center.

Figure 7. *Landerolaria ferresii*. Northern Territory. Photo by Mark Marathon, Wikimedia Commons.

Figure 8. *Landerolaria ferresii*. South Australia. Seeds of South Australia, Conservation Center. Leaves of lower photo show the evenly toothed leaf margins characteristic of the genus.

PHASEOLARIA Nesom, **gen. nov.** **TYPE**: *Phaseolaria elliptica* (DC.) Nesom

Shrubs with large, alternate, petiolate leaves with glabrous, gland-dotted and viscid-resinous surfaces and small heads in corymbs. For Australian botanist Anthony R. Bean.

Shrubs; stem, leaves, and involucres glabrous, glandular, viscid to resinous. **Stems** 0.3–2.5 mm, viscid-glandular. **Leaves** alternate, petiolate, blades narrowly elliptic to lanceolate, oblanceolate, obovate, or ovate, 2.5–11 cm long, petioles 4–17 mm long, not decurrent, venation brochidodromous, margins entire. **Heads** in terminal, corymbose clusters, ultimate peduncles (2–)5–23 mm long, bracteate. **Involucres** short-cylindric, 4.5–6 mm wide (pressed); phyllaries in (2–)3–4 series strongly graduate in length, narrowly elliptic-lanceolate, longest 3–3.5 mm, scarious with a green midregion, glabrous or sparsely hairy distally; receptacles flat to convex, shallowly alveolate. **Ray flowers** fertile, 6–20, ligules white to lilac, 2.2–9 mm long. **Disc flowers** bisexual, fertile, corollas yellow, 3.5–4.5 mm long. **Achenes** subcylindric, slightly compressed, 1.6–3.2 mm long, 4–5-ribbed, sparsely strigose, eglandular; pappus uniseriate, of 15–30 bristles 2.3–5 mm long, or in *P. praetermissa* also with an outer series 0.4–0.5 mm long.

In the molecular-phylogenetic analysis of Cross et al. (2002, Figs. 1 and 3), *Olearia elliptica* and *O. elliptica* "var." *praetermissa* cluster (with low support) in an unresolved position among taxa of Brachyscominae, outside of a more strictly defined *Olearia*. The Lord Howe Island plants ("praetermissa") and a previously undescribed entity ("fulgens") were recognized at specific rank by Bean (2020a), who presented his study as a taxonomic revision of group.

1. Leaves obovate to oblanceolate; ray ligules 2.2–2.6 mm long; achenes 1.6–1.8 mm long; pappus biseriate ..... **Phaseolaria praetermissa**
1. Leaves elliptical to ovate; ray ligules 4.5–9 mm long; achenes 2.1–3.2 mm long; pappus usually 1-seriate.

    2. Leaves 3.6–5.5 times longer than wide; petioles 5–10 mm long; phyllaries glabrous; disc corolla lobes with tiny hairs ..... **Phaseolaria fulgens**
    2. Leaves 2.5–3.5 times longer than wide; petioles 10–17 mm long; phyllaries sparsely hairy at distal end; disc corolla lobes glabrous ..... **Phaseolaria elliptica**

1. **Phaseolaria elliptica** (DC.) Nesom, **comb. nov.** *Olearia elliptica* DC., Prodr. 5: 271. 1836. *Aster ellipticus* DC., Prodr. 5: 271. 1836 [nom. inval., pro syn.]. **LECTOTYPE** (Bean 2020): **New South Wales**. Illawarra, [Oct–Nov 1818], *A. Cunningham 27* (G-DC image, Fig. 1; isolectotype: K).

    Eurybia illita F. Muell., Fragm. 1: 16. 1858. *Aster illitus* (F. Muell.) F. Muell., Fragm. 5: 76. 1865. *Olearia illita* F. Muell., Fragm. 5: 76. 1865 [nom. inval., pro syn.]. **TYPE**: **Queensland**. Moreton District, Mt. Lindesay, no date, *W. Hill s.n.* (holotype: MEL image; isotypes: K-2 collections on one sheet).

2. **Phaseolaria fulgens** (A.R. Bean) Nesom, **comb. nov.** *Olearia fulgens* A.R. Bean, Austrobaileya 10: 658. 2020. **TYPE**: **Queensland**. Darling Downs District, State Forest 595, Talgai, Mount Gammie North, 9 Jan 1993, *D. Halford Q1630* (holotype: BRI; isotypes: MEL, NSW). Types as cited, not seen; line drawing! in protologue.

3. **Phaseolaria praetermissa** (P.S. Green) Nesom, **comb. nov.** *Olearia praetermissa* (P.S. Green) A.R. Bean, Austrobaileya 10: 660. 2020. *Oleolaria elliptica* subsp. *praetermissa* P.S. Green, Kew Bull. 48: 311. 1993. **TYPE**: **New South Wales**. Lord Howe Island, 25 Mar 1971, *A.N. Rodd 1771* (holotype: K image, Fig. 3; isotype: NSW image).

Figure 1. *Phaseolaria elliptica*. Holotype (G-DC).

Figure 2. *Phaseolaria elliptica*. Queensland. *Forster PIF40536* (US).

Figure 3. *Phaseolaria praetermissa*. Holotype (K).

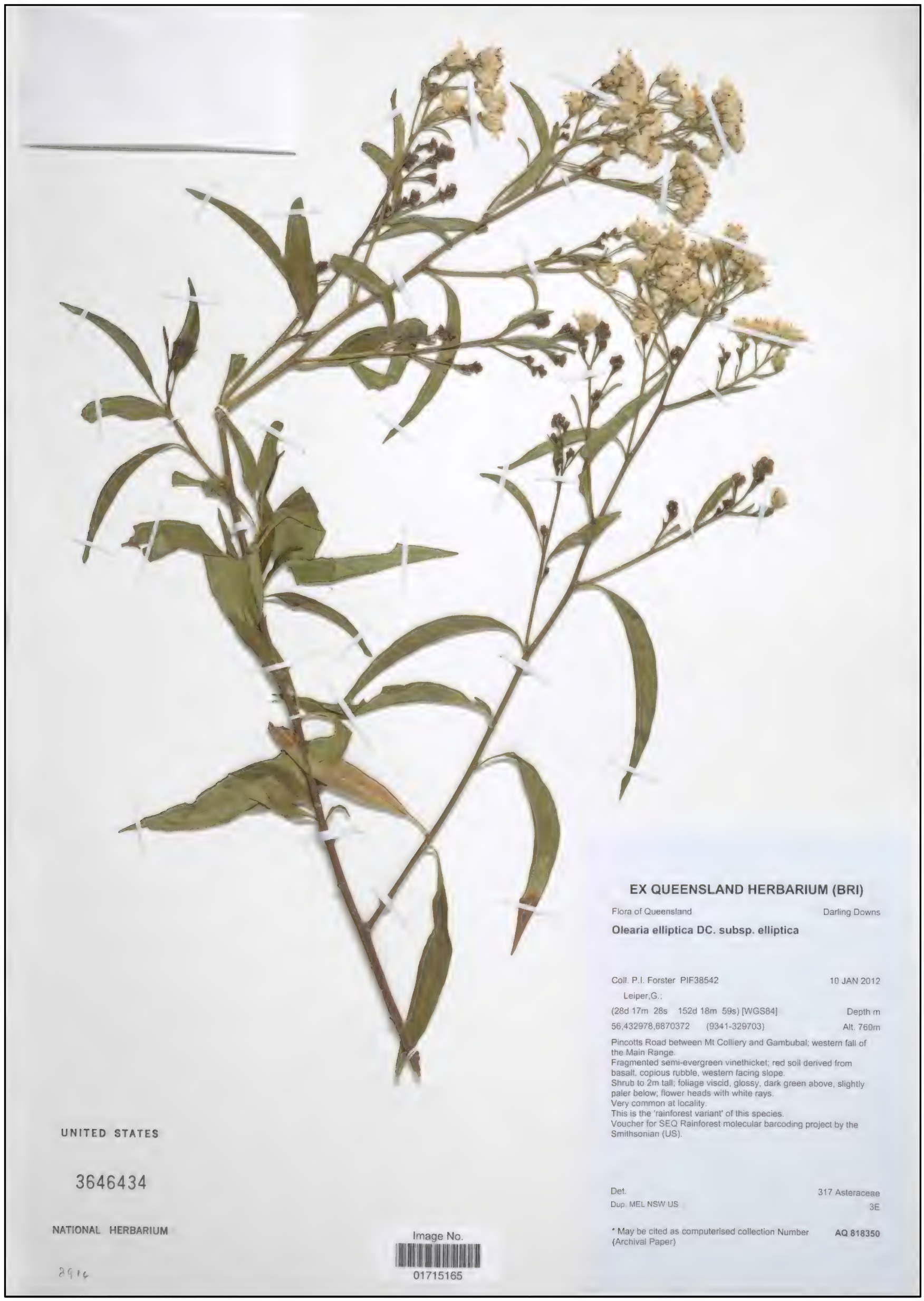

Figure 4. *Phaseolaria fulgens*. Queensland. *Forster PIF38542* (US), cited by Bean (2020).

Figure 5. *Phaseolaria fulgens*. Queensland. *Pedley 5591* (US), cited by Bean (2020).

Figure 6. *Phaseolaria elliptica*. Photo by 'plant.nerd," Flickr.

Figure 7. *Phaseolaria fulgens*. DiversityNativeSeeds.com.au.

Figure 8. Top: *Phaseolaria fulgens*. Photo by Sebastian Tesoriero, Plantthis.com. Bottom: *Phaseolaria elliptica*. New South Wales. Photo by "Brian G," Blue Mountains Native Plants.

Figure 9. *Phaseolaria praetermissa*. Lord Howe Island. Photo by John Game, Wikipedia.

WALSHOLARIA Nesom, **gen. nov. TYPE**: *Walsholaria magniflora* (F. Muell.) Nesom

Distinct in its glabrous, resinous stems, leaves, and involucres, small, thickened, obovate or cuneate leaves with distally few-toothed margins, solitary, terminal heads on short, leafy branches, involucres with multiseriate, elliptic, tightly appressed phyllaries, and oblong, 4-6 ribbed achenes with apically acute pappus bristles. For Australian botanist Neville G. Walsh.

Shrubs; stems, leaves, and involucres glabrous, resinous. **Stems** 0.8–1.5 m. **Leaves** alternate, spatulate to obovate or cuneate, 5–25 mm long, narrowed to a petiolar region, thickened, margins flat, entire to crenate or dentate with a few shallow teeth. **Heads** solitary, terminal on short, leafy branches. **Involucres** cylindric to narrowly ovoid or urceolate, 6–18 mm long; phyllaries linear-lanceolate to elliptic-lanceolate, thickened, in 4–8 tightly appressed series strongly graduate in length; receptacles foveolate. **Ray flowers** 7–24, ligules white to pale purple or mauve, tightly coiling at maturity. **Disc flowers** bisexual, fertile, corollas yellow to cream or (in *W. cuneifolia*) white, narrowly cylindric, 5–10 mm long, lobes triangular, spreading-reflexing. **Achenes** oblong, compressed, 4–6-ribbed, 4–8 mm long, glabrous or loosely strigose-sericeous to sericeous; pappus bristles 1- or 2-seriate (without a short outer series), apically acute, 5–15 mm long, of roughly equal length, slightly longer than the disc corollas.

In the molecular-phylogenetic analysis of Cross et al. (2002), consensus trees indicate that *Walsholaria* is a strongly supported clade phylogenetically distinct from *Olearia*. Figure 1 places it as sister to *Olearia cordata* and *Minuria integerrima*, within subtribe Brachyscominae. Figure 2 (with reduced taxa in *Olearia* sensu stricto) places it as sister to *Olearia* sensu stricto. Figure 3 (with reduced taxa in Celmisiinae) places *Walsholaria* as sister to *Grangea* (Grangeinae) and *Talamancaster panamensis* (Baccharidinae), the whole group as sister to Brachyscominae.

1. Leaves obtriangular; involucres 13–18 mm long; rays 12–24.

   2. Ray ligules 13–22 mm long achenes glabrous; pappus bristles 12–15 mm long ..... **Walsholaria magniflora**
   2. Ray ligules 6–7 mm long; achenes sericeous; pappus bristles 7.5–8 mm long . **Walsholaria cuneifolia**

1. Leaves obovate to obdeltate; involucres 6–12 mm long; rays 7–13, ligules 4–12 or 18–25 mm long; pappus bristles 5–10 mm long.

   3. Ligules 18–25 mm long; achenes 5–6 mm long; pappus bristles 8–10 mm long ..... **Walsholaria calcarea**
   3. Ligules 4–12 mm long; achenes 2.5–4 mm long; pappus bristles 5–8 mm long **Walsholaria muelleri**

1. Walsholaria calcarea (F. Muell. ex Benth.) Nesom, **comb. nov.** *Olearia calcarea* F. Muell. ex Benth., Fl. Austral. 3: 481. 1867. **TYPE MATERIAL**: **New South Wales**. Three collections by *F. Mueller* (MEL 1547084 image, Fig. 1; MEL 1543370; MEL 1543373). Protologue: "Towards Cudnaka and banks of the Murray near Moorundi, *F. Mueller*, (*Herb. F. Mueller*)."

New South Wales, South Australia, Victora, West Australia. Flowering July–September.

"In many respects (leaf size and shape, capitulum size, colour of ray florets) intermediate between *O. muelleri* and *O. magniflora* and perhaps a hybrid between those species, both certainly being present at several sites from which *O. calcarea* has been recorded in Victoria" (Walsh & Lander 1999). It is not convincingly clear, even, that available type material of *O. calcarea* and *O. muelleri* represents different species (pers. observ.). Photos in Figs. 2-5 are identified as on the websites from which they were taken.

2. Walsholaria muelleri (Sond.) Nesom, **comb. nov.** *Eurybia muelleri* Sond., Linnaea 25: 459. 1853. *Olearia muelleri* (Sond.) Benth., Fl. Austral. 3: 481. 1867. *Aster muelleri* (Sond.) F. Muell., Syst. Census Austral. Pl., 78. 1882. **TYPE MATERIAL**: MEL 681594 and 5 collections mounted on a single K sheet. Protologue: "Ad Murray, (Dr. Behr.) In planitie juxta montes Flinders-range et in rupibus ad Cudnaka. Oct."

New South Wales, South Australia, Victora, West Australia. Flowering August–October.

3. Walsholaria magniflora (F. Muell.) Nesom, **comb. nov.** *Aster magniflorus* F. Muell., Fragm. 5(35): 80. 1865 [*Olearia magniflora* cited in synonymy]. *Olearia magniflora* (F. Muell.) Benth., Fl. Austral. 3: 480. 1867. **TYPE MATERIAL**: 1 sheet at K (with 2 collections on the same sheet) and 5 collections at MEL. Protologue: "In planitiebus colibusque desertorum praesertim calcariis secundum flumina Murrumbidgee, Murray's et Darling's River, F.M.; flumen Lachlan's River versus, Burkitt; prope lacum Yanga, Beckler."

New South Wales, South Australia, Victora, West Australia. Flowering (March–)August–October.

4. Walsholaria cuneifolia (Bean & Mathieson) Nesom, **comb. nov.** *Olearia cuneifolia* Bean & Mathieson, Austrobaileya 9: 404. 2015. **TYPE**: **Queensland**. Naipa Downs, ca. 35 km NW of Mitchell, *Eucalyptus thozetiana* woodland on slope rocky mesa, 26 Mar 2015, *M.T. Mathieson MTM1999* (holotype: BRI image; isotypes: CANB, K, MEL image-Fig. 2, NSW, US image).

New South Wales, Queensland, South Australia, Victoria. Flowering August–October.

Figure 1. *Walsholaria calcarea*. Lectotype of *Olearia calcarea* (MEL).

Figure 2. *Walsholaria muelleri*. South Australia. Seeds of South Australia website.

Figure 3. *Walsholaria muelleri*. South Australia. Seeds of South Australia website.

Figure 4. *Walsholaria muelleri*. South Australia. Photo by Ron Taylor, Seeds of South Australia website.

Figure 5. *Walsholaria muelleri*. South Australia. Photo by William Archer, Esperance Wildflowers website.

Figure 6. *Walsholaria magniflora*. South Australia. Seeds of South Australia website.

Figure 7. *Walsholaria cuneifolia*. Isotype of *Olearia cuneifolia* (MEL).

MUELLEROLARIA Nesom, **gen. nov. TYPE**: *Muellerolaria rudis* (Benth.) Nesom

Distinct in its subshrubby habit, vestiture of long, stiff, uniseriate, multicellular, eglandular hairs, sessile leaves, large heads on long, ebracteate peduncles, phyllaries in 2–3 series of equal length, alveolate receptacles, and narrowly cylindric, 6–10-ribbed, glabrous achenes. For Australian botanist Ferdinand von Mueller (1825-1896).

Subshrubs, sometimes aromatic. **Stems** 0.2–1.5 m, woody at base. **Leaves** alternate, sessile to subsessile, subclasping in *M. rudis*, hirsute to strigose-hirsute with uniseriate, multicellular hairs. **Heads** solitary or few on ebracteate or paucibracteate peduncles from distal axils, on peduncles mostly 2–12 cm long and above the level of the leaves. **Involucres** broadly cylindric, 2–4 cm wide (pressed); phyllaries in 2–3 series of equal length, linear-oblong with acute apex, the outer evenly green, sparsely hirsute; receptacles alveolate. **Ray flowers** 20–75, ligules 10–15 mm long; blue to purplish or white, coiling at maturity. **Disc flowers** bisexual, fertile, corollas yellow, 4–5 mm long. **Achenes** narrowly oblong, compressed, 2–3.5 mm long, 6–10-ribbed, glabrous, eglandular; pappus bristles in 2 series, barbellate with acute apices, outer about as long as the disc corollas, inner much shorter.

Olearia picridifolia and *O. rudis* were considered by both Bentham (1867) and Mueller (1865) to be morphologically close, and molecular data (Cross et al. 2002) show strong support for their sister relationship. A strict consensus tree (Fig. 3 of Cross et al.) places *Muellerolaria* as sister to *O. cordata*/ *O. ciliata*/ *Olearia* sensu stricto (clade A); their consensus tree of Fig. 1 places it in an unresolved position among other taxa of Brachyscominae. The two species are distinct in habit and vestiture but the broadly cylindric involucres with linear, equal-length phyllaries mark them as evolutionary sisters.

1. Leaves 6–40 mm wide, sparsely hirsute to glabrate, margins often coarsely serrate ..... **Muellerolaria rudis**
1. Leaves 2–9 mm wide, sparsely to densely hirsute to strigose-hirsute, margins entire ..... **Muellerolaria picridifolia**

1. **Muellerolaria rudis** (Benth.) Nesom, **comb. nov.** *Eurybia rudis* Benth., Enum. Pl. [Endlicher] 58. 1837. *Shawia rudis* (Benth.) Sch.-Bip., Jahresber. Pollichia 18-19: 174. 1861. *Olearia rudis* (Benth.) F. Muell. ex Benth., Fl. Austral. 3: 487. 1867. **LECTOYPE** (designated here): **Western Australia**. Swan River, *Hügel s.n.* (K 838939 image; isolectotype: W image). Protologue: "*Swan-River*. (Hügel.) β) *King Georges Sound*. (Ferd. Bauer.)"

Eurybia scabra Benth., Enum. Pl. [Endlicher] 58. 1837. *Shawia scabra* (Benth.) Sch.-Bip., Jahresber. Pollichia 18-19: 174. 1861. *Olearia rudis* var. *scabra* (Benth.) Benth., Fl. Austral. 3: 487. 1867. **POSSIBLE TYPE**: **Tasmania**. Terra van Diemen, *F. Bauer 27* (W image). Protologue: "s. *Nov. Holl.* (Ferd. Bauer.)."

Aster exsul Lindl., Sketch Veg. Swan River 2: 24. 1839. **TYPE**: (not cited, not seen). As synonym of *Olearia rudis*, fide APNI. Mueller (1865, p. 75) cited this as the locality for *Aster "exul"*: "In collibus nemorosis aridioribus et in planitiebus arenoso-argillaceis dumosis passim a fluvio cygnorum usque ad flumina Darling's River et Wimmera et sinum Rivoli Bay."

Olearia rudis var. *glabriuscula* Benth., Fl. Austral. 3: 487. 1867. **TYPE MATERIAL:** MEL, presumably K). Protologue: "Wimmera, Dallachy; Gawler Town, Rivoli Bay, etc., in S. Australia, F. Mueller."

Roger Fryer has photographed Kangaroo Island plants of *Muellerolaria rudis* with large, sessile glands along the leaf margins (Fig. 10). These almost certainly deserve to be formally recognized.

2. **Muellerolaria picridifolia** (F. Muell.) Nesom, **comb. nov.** *Eurybia picridifolia* F. Muell., Linnaea 25: 397. 1853. *Olearia picridifolia* (F. Muell.) Benth., Fl. Austral. 3: 487. 1867. **LECTOTYPE** (designated here): **South Australia**. Arkaba, 1 Oct 1851, *F. Mueller s.n.* (MEL 1547075 image; isolectotypes: MEL). Protologue: "In fruticetis collium steriliorum inter Rocky-creek et Crystal-brook, nec non in vallibus petraeis prope Arkaba."

Figure 1. *Muellerolaria rudis*. New South Wales. *Crisp 5722* (US).

Figure 2. *Muellerolaria rudis*. Victoria. *Muir 1118* (US).

Figure 3. *Muellerolaria rudis*. Western Australia. *Pritzel 651* (US).

Figure 4. *Muellerolaria picridifolia*. South Australia. *Blaylock 806* (US).

Figure 5. *Muellerolaria rudis*. South Australia. South Australia Seeds website.

Figure 6. *Muellerolaria rudis*. South Australia. South Australia Seeds website.

Figure 7. *Muellerolaria rudis*. Western Australia. Photo by Russell Cumming, Flickriver.

Figure 8. *Muellerolaria rudis*. Western Australia. Photo by Russell Cumming, Flickriver.

Figure 9. *Muellerolaria rudis*. South Australia. South Australia Seeds website.

Figure 10. Kangaroo Island variant of *Muellerolaria rudis*. Photos by Roger Fryer, 28 Dec 2010, North Queensland Plants website.

Figure 11. *Muellerolaria picridifolia*. South Australia. Seeds of South Australia website.

VICINIA Nesom, **gen. nov. TYPE**: *Vicinia ciliata* (Benth.) Nesom

Distinct in its densely arranged, narrow, hirsute to hispid-hirsute, eglandular leaves and solitary heads on long, ebracteate peduncles.

Shrubs or **subshrubs**, taprooted. **Stems** 15–50(–80) cm high, stems and leaves hirsute to hispid-hirsute, eglandular, not viscid, peduncles sparsely cobwebby. **Leaves** densely arranged, often fasciculate, linear to linear-triangular (*V. ciliata*) or spatulate to obovate, elliptic, or oblong-elliptic (*V. squamifolia*), epetiolate, 2–30 mm long, 1–3 mm wide, apex acute or rarely 3-lobed, midvein impressed (sulcate) adaxially, raised abaxially, scabrous to subglabrous above and "rarely with sparse cobwebby hairs" (Flora of Victoria), hairy below, margins entire, narrowly revolute, ciliate. **Heads** solitary, terminal or less commonly terminal and axillary on ebracteate peduncles 5–25(–30) cm long; involucres hemispheric; phyllaries 3(–4)-seriate, linear-lanceolate, graduate in length, green-herbaceous, sometimes purple-tipped, apices acute, hirsute to glabrous, eglandular; receptacles shallowly convex, alveolate. **Ray flowers** 15–35, ligules 10–17 mm long, lilac to blue or violet, coiling at maturity. **Disc flowers** bisexual, fertile, corollas yellow. **Achenes** oblong, compressed, 1.6–3 mm long, 6–10-ribbed, eglandular, variable (see Flora of Victoria website) from glabrous to strigose; pappus of 25–35 barbellate bristles 2.5–4 mm long, subequal, with an outer series of shorter bristles.

In the molecular-phylogenetic analysis by Cross et al. (2002) two consensus trees place *Olearia ciliata* as sister to *Olearia* sensu stricto (clade A of their Figs. 1 and 2). Bentham (1867) placed *Olearia ciliata* in sect. *Merismotriche*, characterized by rigid, uniseriate, multicellular hairs (illustrations in Lander 1990), but the plants are similar in habit to species of *Olearia* sect. *Eriotriche* ("clade A") in their densely arranged, often fasciculate, linear leaves and it produces the "woolly" hairs characteristic of sect. *Eriotriche*. Rigid, eglandular hairs occur in *O. adenophora* and *O. homolepis* of the *O. tenuifolia* group, but the fasciculate leaves and solitary, long-pedunculate heads with narrow phyllaries of *Vicinia* are not found there

1. Leaves mostly 10–30 mm long; involucres 11–14 mm wide (pressed); rays 21–35 .. **Vicinia ciliata**
1. Leaves mostly 2–5 mm long; involucres 7–8 mm wide (pressed); rays 15–26 . **Vicinia squamifolia**

1. **Vicinia ciliata** (Benth.) Nesom, **comb. nov.** *Eurybia ciliata* Benth., Enum. Pl. [Endlicher] 58. 1837. *Shawia ciliata* (Benth.) Sch.-Bip., Jahresb. Pollichia 18/19: 174. 1861. *Aster huegelii* F. Muell., Fragm. 5(35): 79. 1865. *Olearia ciliata* (Benth.) F. Muell. ex Benth., Fl. Austral. 3: 488. 1867. **LECTOTYPE** (designated here): **Australia**. Nova Hollandia, *F. Bauer "20 & 28"* (W 46602 image, fragment MEL image). SYNTYPE: King George's Sound, *C.A.A. Hugel s.n.* (W 46603).

   Mueller did not cite a type for *Aster huegelli*. He cited *Eurybia ciliata* Benth. a synonym, thus it seems that he intended *Aster huegelii* as a replacement name in *Aster* for *Eurybia ciliata* (not *Aster ciliatus* Walt. 1788, Willd. 1803, or Nutt. 1840).

   Olearia ciliata var. *hispida* Benth., Fl. Austral. 3: 488. 1867. **TYPE**: **South Australia**. In fruticitis apud Hake's Place, 21 Sep 1848, *F. Mueller s.n.* (holotype: MEL image).

   Eurybia ciliata var. *glabrata* Sond., Linnaea 25: 458. 1853. Protologue (localities from South Australia and Tasmania): "β. glabrata, foliis glaberrimis vel ima basi ciliolatis achaenniisque glabris. Pine forest ad Gawler et prope Pfeiffer's Station, Januar. Dr. (Behr.) North-rhine September. Ad fluv. Onkaparinga. Van Diemensland (Stuart.) β ad Port Lincoln." Not seen.

   South Australia, Tasmania, Victoria, Western Australia. Flowering August-November (December).

2. **Vicinia squamifolia** (F. Muell.) Nesom, **comb. nov.** *Aster huegelii* var. *squamifolius* F. Muell., Fragm. 5(35): 79. 1865. *Olearia ciliata* var. *squamifolia* (F. Muell.) Benth., Fl. Austral. 3: 488. 1867. **LECTOTYPE** (desgnated here): **South Australia**. Kangaroo Island, Cygnet Bay, no date, *Fr. Waterhouse s.n.* (MEL 1543684; isolectotype: K). Mueller' protologue cited the locality as

"ex insula halmaturorum;" Bentham cited "Kangaroo Island, Waterhouse." There are two labels and apparently two Waterhouse collections on the MEL sheet — it is not clear which collection goes with which label. The second label has "[Kangaroo Island], Scrub near Wallans Hut, no date, *F. Waterhouse s.n.*" As an extension of the lectotypification, the two taller stems on the right are associated here with the Cygnet Bay label.

Endemic to Kangaroo Island. Flowering September-December.

Figure 1. *Vicinia ciliata*. Top: Victoria. Flora of Victoria website. Bottom: South Australia. Seeds of South Australia website.

Figure 2. *Vicinia ciliata*.

Figure 3. *Vicinia ciliata*. Victoria. Photos by Geoff Carle (top), Annabel Carle (bottom). Flora of Victoria website.

Figure 4. *Vicinia ciliata*. Victoria. Photo by Lorraine Jansen, Flora of Victoria website. "Eriotriche" hairs on the peduncle.

Figure 5. *Vicinia ciliata*. Top: Seeds of South Australia website. Bottom: South Australia. Photo by Reiner Richter, iNaturalist.

Figure 6. *Vicinia ciliata*. South Australia. Detail from holotype of *Olearia ciliata* var. *hispida* (MEL).

Figure 7. *Vicinia ciliata*. Left, old terminal heads overtopped by heads from new growth. Right, details of leaves from the same plant. "S.W. Australia." *Mueller 136* (PH).

Figure 8. *Vicinia ciliata*. Victoria. Photo by Loraine Jansen, Flora of Victoria website.

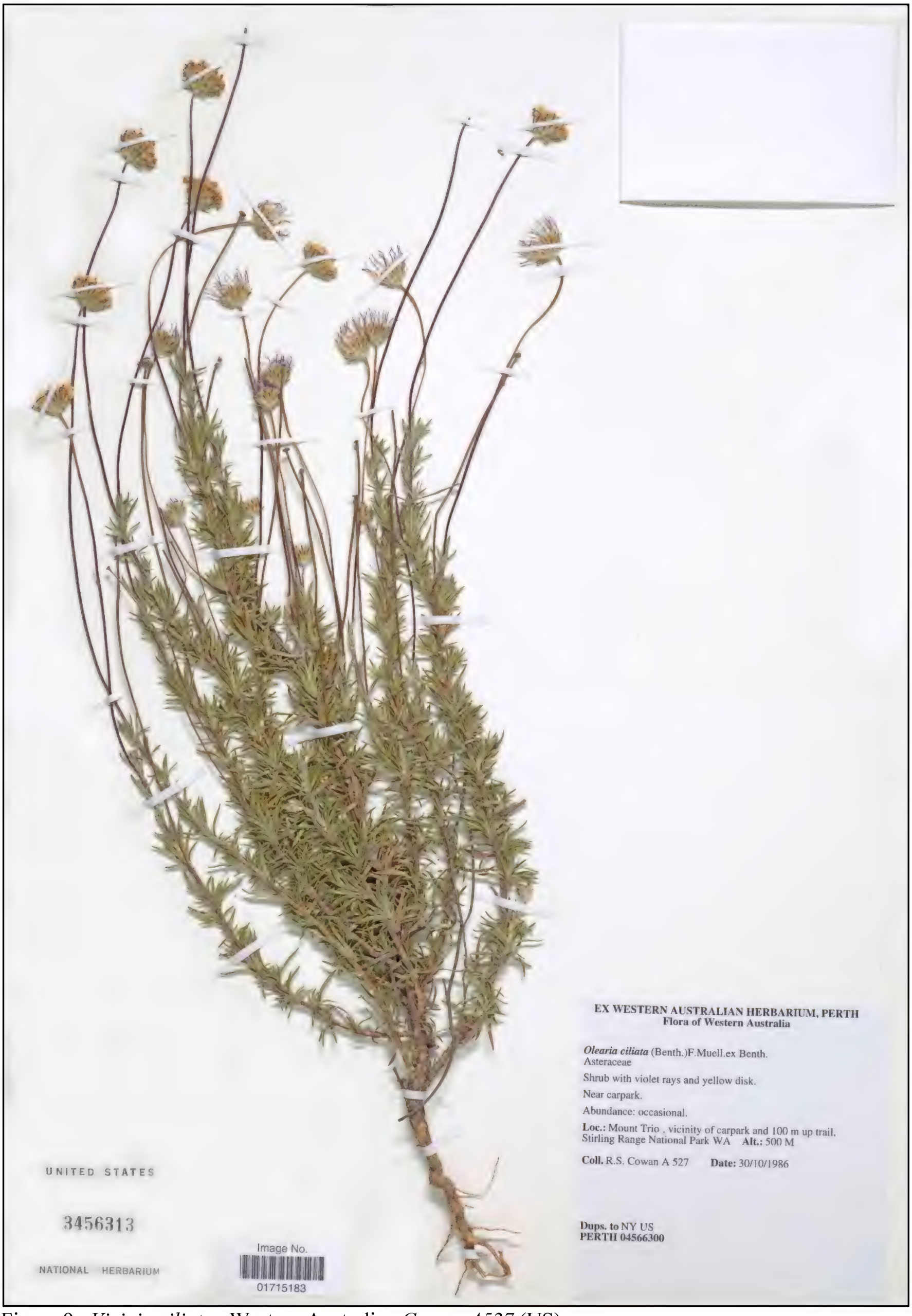

Figure 9. *Vicinia ciliata*. Western Australia. *Cowan A527* (US).

Figure 10. *Vicinia ciliata*. Victoria. *Muir 935* (US).

Figure 11. *Vicinia squamifolia*. Seeds of South Australia website.

Figure 12. *Vicinia squamifolia*. Seeds of South Australia website.

Figure 13. *Vicinia squamifolia*. Kangaroo Island. Syntype of *Aster huegelii* var. *squamifolius* (MEL 1543685).

WOLLEMIASTER Nesom, **gen. nov.** **TYPE**: *Wollemiaster cordatus* (Lander) Nesom

Distinct in its shrubby habit, densely stipitate-glandular vestiture, epetiolate, narrowy oblong leaves with an ampliate base, and few, solitary heads terminal and axillary on leafy branches.

Shrubs, aromatic; stems, peduncles, and leaf surfaces densely stipitate-glandular with biseriate hairs, with less conspicuous uniseriate, erect, eglandular hairs and appressed uniseriate hairs with a long, flexuous apical cell. **Stems** 1–2 m. **Leaves** alternate, linear-oblong to lanceolate-oblong, epetiolate, 2.5–4 cm long, 4–8 mm wide, base ampliate and subclasping, midvein impressed (sulcate) adaxially, raised abaxially, margins entire, revolute. **Heads** solitary and few, terminal and axillary on leafy branches. **Involucres** campanulate, 8–9 mm wide (pressed); phyllaries 3–4-seriate, graduate in length, lanceolate, longest 4.5–5.5 mm, scarious with a green midregion, stipitate-glandular, apex acuminate. **Ray flowers** 12–18, ligules white to pale blue or violet, ca. 12 mm long, coiling at maturity. **Disc flowers** bisexual, fertile, corollas 4–5 mm long, yellow. **Achenes** oblong, compressed, ca. 2.5 mm long, 6-ribbed, strigose, eglandular; pappus uniseriate, of 35–40 barbellate bristles 1–3.5 mm long, about 3/4 as long as the disc corolla tube and limb.

1. **Wollemiaster cordatus** (Lander) Nesom, **comb. nov.** *Olearia cordata* Lander, Telopea 1: 84. 1975.
TYPE: **New South Wales.** 0.5 mi above Wisemans Ferry on road to Maroota, near road notice "Trucks use low gear," Mar 1973, *P. Matthew NSW128087* (holotype: NSW not seen; isotype: K image, Fig. 1).

New South Wales. "Most known populations occur within conservation reserves (Wollemi National Park, Yengo National Park, and Wisemans Ferry Historic Site)" (New South Wales Office of Environment & Heritage). Flowering mostly February-June, less commonly throughout the year.

Wollemiaster cordatus has "Eriotriche hairs" and the general habit of linear-leaved species of sect. *Eriotriche*, where it is most similar in habit to the *O. tenuuifolia* group, but the dense, stipitate-glandular vestiture is not known among those species or elsewhere. In the molecular analysis of Cross et al. (2002), a strict consensus tree (their Fig. 1) shows *Olearia cordata* as sister to *Minuria integerrima*. In a consensus tree with a reduced number of Celmisiinae species (their Fig. 3), *O. cordata* is sister to *O. ciliata* and "clade A."

Figure 1. *Wollemiaster cordatus*. Detail from K isotype (Fig. 2).

Figure 2. *Wollemiaster cordatus*. New South Wales. K isotype.

Figure 3. *Wollemiaster cordatus*. New South Wales. Earth.com, no attribution of photographer,

EOGLANDULA Nesom, **gen. nov.** **TYPE**: *Eoglandula glandulosa* (Labill.) Nesom

Distinct in its slender, glabrous, sessile-glandular stems, linear leaves with nodular-glandular swellings along the margins, and small heads in corymbs or panicles.

Shrubs (short-lived?) or **subshrubs**. **Stems** 1–2.5 or 0.4–0.7 m, sessile-glandular; internodes 2–5 mm long; in *E. glandulosa*—axillary buds apparently absent, leaf axils (lower half of stem) producing cluster of small leaves or (upper half) branches bearing an inflorescence. **Leaves** alternate (spiral), blades linear, epetiolate, 5–55 mm long, 1–2 mm wide, glabrous, resinous, venation indistinct, apex acute, margins with prominent nodular-glandular swellings. **Heads** in terminal corymbs, ultimate peduncles 3–15(–20) mm long. **Involucres** shallowly campanulate-cylindric, 3–4 mm wide (pressed); phyllaries lanceolate-elliptic to elliptic-lanceolate, thick-herbaceous, (2–)3–4 seriate, graduate in length, longest 1.8–2.4 mm long; receptacles shallowly convex, alveolate. **Ray flowers** fertile, 8–25, ligules 4–9 mm long, white or pale blue, tightly coiling at maturity. **Disc flowers** bisexual, fertile, corollas yellow, 2.5–2.8 mm long, tube gradually broadening into the limb, lobes narrowly triangular, recurving-coiling. **Achenes** elliptic to oblanceolate-elliptic, 1.2–1.8 mm long, slightly to strongly compressed, 3–5-ribbed, sparsely short-strigose with Zwillingshaare (paired cells divergent at the apex in *E. glandulosa*?) or densely strigose-sericeous, eglandular; pappus 1-seriate, of 35–54 barbellate bristles 2–2.5 mm long, apices clavate (*E. glandulosa*) or acute (*E. suffruticosa*).

In the molecular analysis of Cross et al. (2002), a strict consensus tree (their Fig. 1) places *Olearia glandulosa* in an unresolved position among taxa of Brachyscominae. Another consensus tree (their Fig. 3, after reduction of taxa of Celmisiinae) places it as basal to subtr. Brachyscominae. *Olearia suffruticosa* is remarkably different from *O. glandulosa* in growth form, but even the habit of *O. glandulosa* is unusual, with its long, slender, proximally unbranched stems. An unambiguous characterization of the above-ground duration of the latter has not been published. The glandularity of the two species is so distinct, however, otherwise unknown in Brachyscominae, that a sister relationship is highly probable.

1. Shrubs; stems 1–2.5 m tall; leaves 5–55 mm long; heads in distinct corymbs, on bracteate peduncles; achenes sparsely strigose ..... **Eoglandula glandulosa**

1. Subshrubs; stems 0.4–0.7 m tall; leaves mostly 1.5–6(–14) mm long; heads in panicles, on leafy, peduncular branches; achenes densely strigose-sericeous ..... **Eoglandula suffruticosa**

1. Eoglandula glandulosa (Labill.) Nesom, **comb. nov.** *Aster glandulosus* Labill., Nov. Holl. Pl. 2: 50, t. 197. 1806. *Galatella glandulosa* (Labill.) Nees, Gen. Sp. Ast., 174. 1832. *Eurybia glandulosa* (Labill.) DC., Prodr. 5: 269. 1836. *Shawia glandulosa* (Labill.) Sch.Bip., Jahresb. Pollichia 18/19: 173. 1861. *Olearia glandulosa* (Labill.) Benth., Fl. Austral. 3: 454. 1867. **TYPE**: **Tasmania**. Protologue: "In capite Van-Diemen," *J.J.H. Labillardiére s.n.* (holotype: FI 6203 image; isotypes: FI image, G-2 sheets-images, P image).

Australian Capital Territory, New South Wales, South Australia, Tasmania, Victoria. Flowering October–April.

2. Eoglandula suffruticosa (D.A. Cooke) Nesom, **comb. nov.** *Olearia suffruticosa* D.A. Cooke, J. Adelaide Bot. Gard. 7: 279. 1985. **TYPE**: **South Australia**. Bool Lagoon, Hundred of Robertson, ca. 25 km S of Naracoorte, 7 Apr l963, *D. Hunt 1545* (holotype: AD image, Fig. 9).

Southeastern South Australia, southwestern Victoria. Flowering March–May.

Cooke (1985, p. 279) noted that "This species is closely related to *Olearia glandulosa* but is readily distinguished by the subshrubby habit, loose leafy inflorescence, and larger capitula. The two species are sympatric and occur in similar habitats, but no transitional specimens have been seen and they have distinct flowering periods … ."

Figure 1. *Eoglandula glandulosa*. Victoria, Macedon Ranges. Photo by Russell Best, Atlas of Living Australia website <ala.org.au/species>.

Figure 2. *Eoglandula glandulosa*. New South Wales. *Wilson 561* (US).

Figure 3. *Eoglandula glandulosa*. Photo by David Francis, Wikimedia Commons.

Figure 4. *Eoglandula glandulosa*. Details from FI isotype.

Figure 5. *Eoglandula glandulosa*. Australian Capital Territory, Namadgi National Park. Canberra Nature Map website. <https://canberra.naturemapr.org/>

Figure 6. *Eoglandula glandulosa*. Details from FI isotype.

Figure 7. *Eoglandula glandulosa*. New South Wales. Photo by Andrew Ome, New South Wales Flora Online-PlantNET.

Figure 8. *Eoglandula glandulosa*. South Australia. Seeds of South Australia, South Australian Seed Conservation Centre, Botanic Gardens of South Australia.

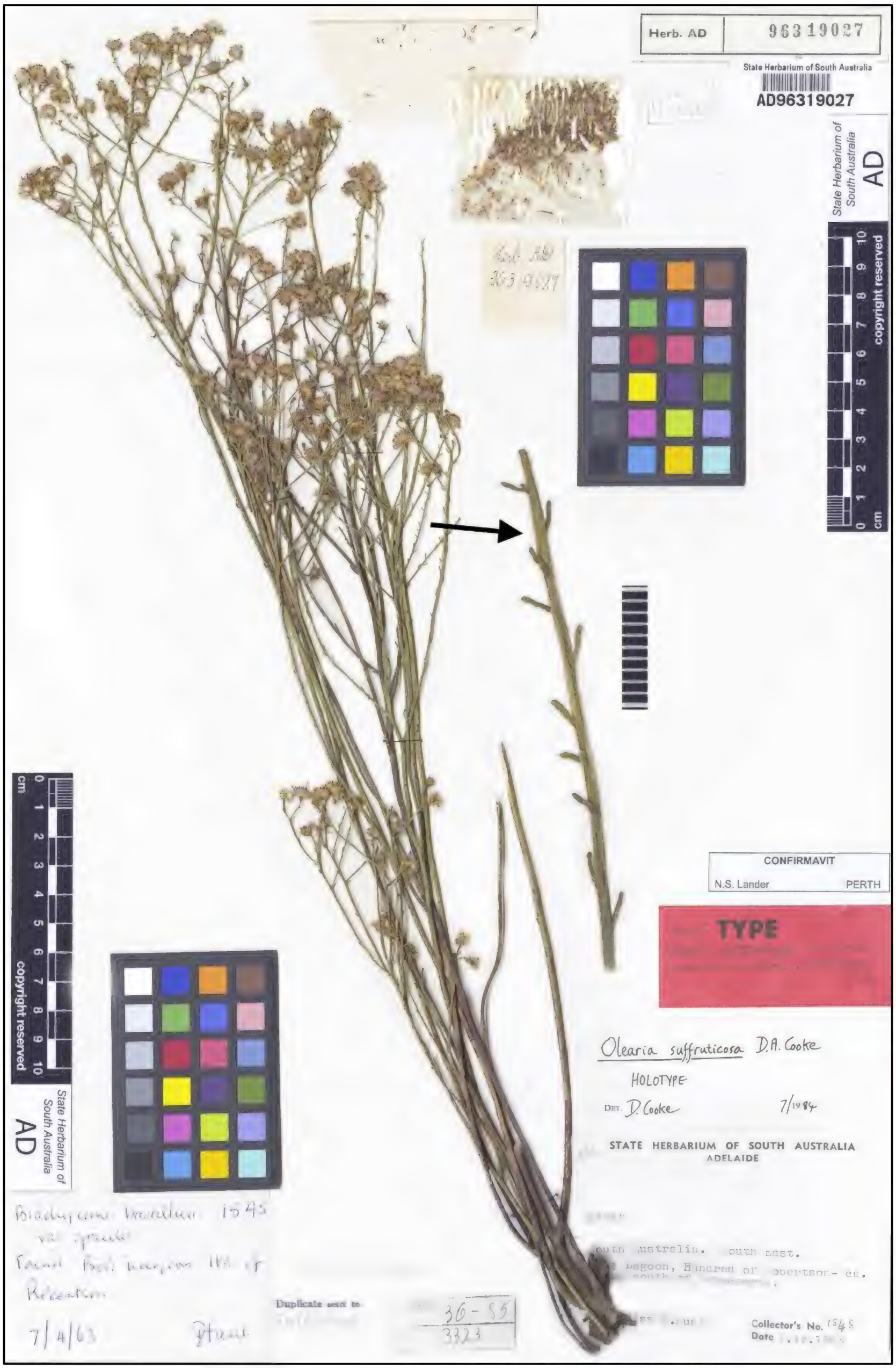

Figure 9. *Eoglandula suffruticosa*. Holotype (AD).

Figure 10. *Eoglandula suffruticosa*. Details from the holotype.

Figure 11. *Eoglandula suffruticosa*. South Australia. Seeds of South Australia website.

Figure 12. *Eoglandula suffruticosa*. South Australia. Seeds of South Australia website.

Figure 13. *Eoglandula suffruticosa*. South Australia. Seeds of South Australia website.

Figure 14. *Eoglandula suffruticosa*. Royal Botanic Gardens Melbourne. Photo by Melburnian, Wikipedia.

Figure 15. *Eoglandula suffruticosa*. South Australia. Seeds of South Australia website.

LINEALIA Nesom, **gen. nov.** **TYPE**: *Linealia flocktoniae* (Maiden & Betche) Nesom

Distinctive in its tall habit with stems mostly unbranched up to near the inflorescence, short duration and lack of secondary growth, eglandular vestiture, linear leaves on short internodes with dense axillary clusters of slightly smaller ones, heads in terminal corymbs, and relatively small achenes.

Short-lived perennial herbs, evergreen, living up to 4-5 years, probably taprooted (see below). **Stems** 1–2.5 m high, green, without secondary growth or axillary buds, single or much-branched from the base, mostly unbranched up to the inflorescence, internodes 2–15 mm long, sparsely and minutely puberulent with crisped, eglandular hairs, eglandular. **Leaves** linear, epetiolate, crowded, alternate (spiral) and with clusters of leaves from axils, 2–9 cm long, 1–5 mm wide, apex acute, margins strongly revolute, entire, abaxial venation pinnate, surfaces sparsely and finely pubescent, glabrescent, eglandular. **Heads** in terminal corymbs; ultimate peduncles 15–40(–50) mm long. **Involucres** short-cylindric, 4–5 mm high, 7–8.5 mm wide (pressed); phyllaries green-herbaceous, thickened, linear-lanceolate, apices acute-acuminate, in 2–3 series, inner of ca. equal length, outer about about half the length of the inner; receptacles shallowly convex, shallowly foveolate. **Ray flowers** 30–48 in 1(–2) series, ligules ca. 6–8 mm long, white to light violet, coiling at maturity. **Disc flowers** bisexual, fertile, corollas yellow, 4.5–5 mm long, tube nearly filiform, ca. half the length of the corolla, abruptly broadening into the cylindric limb, 5-lobed, lobes triangular, spreading. **Achenes** elliptic-oblong, 1.8–2 mm long, compressed, ca. 6–8-nerved, strigose-sericeous, eglandular; pappus 1-seriate, of 36–50 persistent, apically acute barbellate bristles equalling the disc corolla length.

Linealia flocktoniae (Maiden & Betche) Nesom, **comb. nov.** *Olearia flocktoniae* Maiden & Betche, Proc. Linn. Soc. NSW 34: 361. 1909. **TYPE**: **AUSTRALIA**. **New South Wales**. Dorrigo, Mar 1909, *J.L. Boorman s.n.* (holotype: NSW 179624; isotypes: MEL image, NSW-2 sheets, PERTH). Holotype fide Australasian Virtual Herbarium.

In the molecular-phylogenetic analysis of Cross et al. (2002), a consensus tree (their Fig. 1) places *Olearia flocktoniae* in an unresolved position among taxa of subtr. Brachyscominae. A second consensus tree (their Fig. 3, with reduction of species in Celmisiinae) places it as most closely related to *Kippistia suaedifolia*, *Minuria cunninghamii*, and *Minuria* sp., this group in turn as sister to *Tetramolopium alinae*, *Peripleura bicolor*, and *Vittadinia*. *Linealia* resembles *Eoglandula* and some species of "clade A" sect. *Eriotriche* in its linear, congested leaves and corymboid inflorescence.

These plants have been characterized as "shrubs," "short-lived shrubs," "non-woody shrubs," and "short-lived, semi-herbaceous shrubs" — their habit is difficult to categorize. Maiden and Betche (1909) noted in the protologue that "The collector asserts that it is an annual," the rationale unstated but presumably because (at least in part) of the green stems and apparent lack of secondary growth. The plants are evergreen but without secondary growth and plants have not been observed to live more than four or five years. They reach reproductive maturity in the second year, growing taller and flowering more abundantly with addition of inflorescence branches in the 3rd and 4th years (Gross & Mackay 2014).

Below-ground parts of *Linealia* apparently have not been characterized, but *Kippistia suaedifolia* (subshrubs) and *Minuria cunninghamia* (perennial herbs) are taprooted and it is plausible that *Linealia* is also.

Linealia plants grow adjacent to wet sclerophyll forest and warm-temperate rainforest, but even so the flowering period apparently is constrained to the five months from January to May, perhaps reflecting ancestry from a less equable climate (NSW DEC 2004). They grow only in disturbed sites (roadsides, openings, clearings) and competition with other species hastens their demise.

Figure 1. *Linealia flocktoniae*. New South Wales. Photo by Shane Ruming, New South Wales Office of Environment & Heritage, Threatened Species.

Figure 2. *Linealia flocktoniae*. New South Wales. New South Wales Office of Environment & Heritage, Threatened Species. Top: Photo by Shane Ruming. Bottom: Photo by Peter Richards.

Figure 3. *Linealia flocktoniae*. Isotype (MEL).

Figure 4. *Linealia flocktoniae*. Detail from isotype (MEL).

Figure 5. *Linealia flocktoniae*. Details from isotype (MEL).

Figure 6. *Linealia flocktoniae*. Details of stems, leaves, and nodes from isotype (MEL).

EPHEDRIDES Nesom, **gen. nov.** **TYPE**: *Ephedrides trifurcata* (Lander) Nesom

Distinct in its low, subshrubby habit with spreading woody rhizomes or underground caudex branches, glabrous-viscid vestiture, opposite branching, bracteate leaves, and solitary, few-flowered heads.

Subshrubs, tussock-like or in patches, from woody rhizomes or underground caudex branches; vegetative surfaces pustulate and viscid but otherwise glabrous. **Stems** mostly 20–30 cm, branches opposite, rarely with secondary branches, without secondary growth. **Leaves** opposite, all cauline, bracteate, indurate and brownish, deltate to triangular or oblong-triangular, 1–5.5(–8, fide protologue) mm long, margins entire. **Heads** solitary, terminal. **Involucres** narrowly ovoid, 2.5–3.8 mm wide (pressed); phyllaries ca. 3-seriate, elliptic-ovate to elliptic, graduate in length, longest 5–6 mm, indurate-stramineous with a darker, slightly keeled midline, margins membranous; receptacle shallowly convex. **Ray florets** 2–4, ligules 4.5–5 mm long, white. **Disc florets** bisexual, fertile, 3, corollas 5–5.7 mm long, white to cream, lobes narrowly triangular, reflexing. **Achenes** obovoid, 1.7–2.3 mm long, sericeous with duplex hairs; pappus uniseriate, of 40–52 barbellate bristles more or less equal in length to the disc corollas.

Ephedrides trifurcata (Lander) Nesom, **comb. nov.** *Olearia trifurcata* Lander, Nuytsia 18: 101. 2009.

TYPE: **Western Australia**. Ca. 1 km SE of Kau Rock, ca. 60 km NE of Esperance, 33° 24' 35", 122° 19' 53", margin of playa lake, *Stipa* sp. zone with *Eucalyptus* sp. and *Melaleuca* spp., occupies ca. 4-5 hectares, 3 Jan 1990, *W.R. Archer s.n.* (holotype: PERTH image, Fig. 1; isotypes: AD, CHR, K, MEL).

South-central Western Australia, mostly at margins of playa lakes and saline drainages. Flowering November-March.

These plants are highly unusual in growth habit and morphology. Small, white-flowered heads apparently have evolved independently in several olearioid lineages. The species has not been included in molecular sampling.

Figure 1. *Ephedrides trifurcata*. Photos by W.R Archer, FloraBase, the Western Australia Flora.

Figure 2. *Ephedrides trifurcata*. Western Australia. Holotype (PERTH).

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THREE FACTORS OF "PLANTNESS" — TRAIT SUMMARY SCORES GENERATED FROM A BIFACTOR MODEL WITH COMPLEX STRUCTURE

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ABSTRACT

This paper explores whether a data reduction technique used almost exclusively in psychometrics — i.e., bifactor latent trait modeling — provides any added value beyond unsupervised machine learning techniques already common in plant science. Using data from the TRY database and other public repositories, for 52,104 species I compiled 42 wide-ranging plant traits (e.g., growth form, plant height, leaf size, leaf dry mass, leaf phosphorus, vessel and fiber length, seed size, medicinal use, geographic distribution, protected species status, etc.) and conducted Exploratory Factor Analysis (EFA) with iterated target rotation to explore how the traits "cluster." Three factors were identified in the EFA, later modeled in a Quasi-Confirmatory Factor Analysis (CFA) using a bifactor configuration specifying three specific factors. The three factors could reasonably be called Leaf Size (defined most strongly by leaf dry and fresh mass), Vessel/Fiber Length, and SLA/Water Content (defined most strongly by specific leaf area, leaf water content, and the inverse of leaf dry matter content). The statistical model used to describe these three factors —i.e., the "bifactor" model— is named as such because each trait belongs to not only its specific factor (e.g., the trait "leaf fresh mass" belongs to the Leaf Size factor) but also to an overall "General" factor to which all traits belong. That is, in addition to the three factors from the article's title, there is a "fourth factor" (the General Factor of Plantness, or simply General Plantness) comprising all traits. The meaning of General Plantness (indicated most strongly by water content, plant height, and possibly tree/shrub form) is unclear without genetic research, and it is not one of the three factors of plantness. Rather, General Plantness would better be conceptualized as a "meta-factor" transcending the three factors of plantness from the title. I speculate that the General Factor of Plantness is a latent measure of genome age, or how long ago a species evolved to its current form.

The three factors of plantness (Leaf Size, Vessel/Fiber Length, and SLA/Water Content), along with the General Factor of Plantness, are plotted with examples and discussed. Examples included common (e.g. willow tree, fleabane), cultivated (e.g. corn, watermelon), unusual (e.g. venus fly trap, ginkgo), and scientifically well-known (e.g. thale cress, *Amborella*) species. Importantly, the examples were chosen independently of the traits or trait scores (to avoid choosing an example **because** it had a specific score). Of the examples, *Ephedra distachya* had the highest score on Vessel/Fiber Length, *Ginkgo biloba* had the highest score on SLA/Water Content, and *Zea mays* (corn) had the highest score on Leaf Size. The species *Amborella trichopoda*, *Cycas revoluta*, and *Ginkgo biloba* had the highest scores on General Plantness. The lowest scores on General Plantness were found in *Arabidopsis thaliana*, *Dionaea muscipula*, and *Papaver rhoeas*. Genome age is a common factor among the three species highest on plantness, suggesting that the General Factor of Plantness deserves further investigation. Critically, scores are provided (link below) for N = 52,104 species, many of which have scores more extreme than the few examples reported above. Further research using genetic data is strongly encouraged.

When measuring plant traits (e.g. leaf length, root depth, etc.), whether with a ruler or mass spectrometer or simple scale, it is common to take many related measurements. Especially in large-scale studies (Fiorani & Schurr 2013; Pieruschka & Schurr 2019; Zhang et al. 2019), many measurements of many traits are recorded. The result is often a data matrix where each row is a species and each column is a measurement (trait), such as leaf length or root depth. While this data matrix may be sufficient to answer the researcher's question, it contains much more information that is often discarded: meaningful patterns in the bivariate (1-on-1) relationships among the measurements. A

whole branch of statistical methodology, unsupervised machine learning, is dedicated to uncovering such patterns, including in data characterizing plants and plant species.

Here, I explore whether a data reduction technique used almost exclusively in psychometrics — i.e., bifactor latent trait modeling — provides any added value to techniques already common in plant science (Chitwood & Topp 2015; Elavarasan et al. 2018; Feldmann et al. 2020; Furbank et al. 2019; Mendes et al. 2019; Saryan et al. 2020; Zhao et al. 2018; also see Butler et al. 2017). The idea behind data reduction techniques (elaborated below) is to start with a set of trait measurements (e.g., physical and chemical features) and determine which measurements are of traits that correlate with each other relative strongly, with the purpose of grouping them (not the species) into categories. For example, four traits might be root length, root thickness, phosphorus per mass of stem, and phosphorus per mass of leaf. Using the 4x4 matrix of bivariate relationships (often a correlation matrix with 1s on the diagonal and strengths of relationships ranging from -1 to 1 off the diagonal), most data reduction algorithms will "detect" that the first two traits (having to do with root size) are measurements of things that tend to correlate with each other more than with the things measured in the other two variables. Likewise for the latter two traits (having to do with phosphorus concentration) — the algorithm will detect that they are measurements of things that tend to correlate with each other more than with the two root-related variables. The result will be that the four variables have been "reduced" to two variables, one related to root size and another related to phosphorus concentration. Going from four to two variables is not very interesting or useful, but going from dozens or hundreds of variables to a much smaller number might provide interesting insights or at least serve a practical purpose for future researchers (see below). The technique used here is called "factor analysis."

Factor analysis is a type of data reduction technique ("unsupervised machine learning technique" is equivalent) that groups variables (plant traits in this case) into clusters according to some goal[1]. It is usually motivated by one of two goals.

1) Data reduction. Reducing the number of total variables used in analysis by creating (called "deriving") a smaller number of variables that combine information from the many variables. For example, if trying to use house characteristics to predict future selling price, one might have the following nine variables: square footage, number of bedrooms, number of bathrooms, cost of refrigerator, cost of oven, cost of microwave, neighborhood mean rents (1BR), school district quality score, and mean credit rating of neighborhood residents. Before running any analyses, in this very simple case, one could intuitively group the above variables into three categories—house size, appliance quality, and location desirability. This reduction in the number of variables is advantageous for reasons beyond the present scope, but also for the simple reason that it is more parsimonious. Importantly, in the above case, it is easy to intuit how the variables should group, but in many applied cases involving dozens or hundreds of variables, it is not possible for a human to reasonably group the variables into clusters. This is the purpose of factor analysis: using the data alone, the algorithm groups variables optimally without any input from the researcher except how many factors to extract (in the above example, three).
2) Theory testing. Testing or developing a theory based on some a priori expectations. For example, in psychometrics, one might have a hypothesis about how mental abilities tend to correlate — e.g., that tests of reading comprehension will tend to correlate more strongly with other verbal tasks than with quantitative tasks. This could be tested using factor analysis, because, if the theory generating the hypothesis is true, then a group of tests factor analyzed should cluster according to verbal-versus-quantitative rather than some other classification scheme (e.g. self-paced versus not, multiple-choice

[1] In factor analysis specifically, the algorithm usually seeks a solution that has "simple structure", which is a set of rules defined by Thurstone (1947) listing out the characteristics of a matrix of numbers that is most likely to be interpretable by humans. That is, the "optimum criterion" is a solution that is most interpretable to humans, where interpretable is defined by a set of logical rules that can be interpreted by a computer (e.g., must be a specific number of zeros in each row). This ability to tell a computer what is interpretable (called "factor rotation") was one of the most important developments in psychometrics.

versus free response, etc.). An example, again from psychometrics, is the idea that psychiatric disorders and symptoms can be explained by a specific theory (Lahey et al. 2017) that can draw evidence (Lahey et al. 2012) from factor analysis.

Study Purpose

The current study is motivated mostly by #1 above, data reduction, insofar as I wish to generate a small set of phenotype scores for plant researchers, but #2 (theory generation or testing) is also relevant insofar as a secondary question of the study is whether the General Factor of Plantness has any meaning. The term "General Plantness" is admittedly opaque—after all, how could one species of plant have more "plantness" than another species of plant? Until further studies are done to investigate the phenomenon, I simply have no better name. Whatever it is, General Plantness is a dimension that runs through all plants, a latent meta-trait influencing all traits in all three factors mentioned in the title of this article. To be more concrete, I speculate that the General Factor of Plantness is a combination of genes that evolved early in plant evolution and therefore tend to have more relative influence in "old" plants—i.e. plants that evolved to their present form early. I present for testing the idea that there is a group of genes that collectively determine (including gene-gene interactions) the traits that are strongly associated with the General Factor of Plantness, and these genes will be evolutionarily old. This claim could easily be tested in a genome-wide association study (GWAS) using the General Plantness score, though I would like to emphasize the importance of gene-gene interactions in this case. I therefore recommend that geneticists identify *a priori* the genes known to be "old" and include interactions among them in the GWAS; this, as opposed to approaching it from the other way, starting with the plants that we already know are old in form. Regardless, this is a theoretical question that will be answered only by genetic data, and once further research into the General Factor of Plantness is completed, perhaps it will be renamed to better reflect what it is actually capturing. However speculative, a strength of the above claim is the falsifiability: the only feasible explanation for a General Factor of Plantness to exist is that the various sizes of loadings on the general factor are caused by a specific constellation of genes and their interactions; otherwise, General Plantness does not exist. For this reason, in addition to the bifactor scores I provide, I also provide the analogous scores using the exact same method minus the bifactor component (no general factor). Even if it does turn out that the bifactor scores are suboptimal, the correlated-traits scores will still be usable. Scores are available at <https://www.mooremetrics.com/3fp/>.

METHODS

Data and sources

Data were obtained from the TRY database (32 traits from the main database; Kattge et al. 2011, 2020), growth form data from the GIFT database (Weigelt, König, & Kreft 2020), protected status data from the IUCN "Red List" (Species Survival Commission 2001-2020), "climber" status data from the Jena experiment (Roscher et al. 2018), and medicinal use data collected firsthand from multiple public sources (European Medicines Agency 2020; Wikipedia.org 2020; World Health Organization 2007). The data set used here includes a total of 52,104 species and 42 traits (listed in Table 1). Factor scores available at <https://mooremetrics.com/3fp/>.

TRY database. The relevant trait data in the TRY database can be represented by a two-dimensional matrix: the species × trait matrix, with species in rows and traits in columns. It is large but sparse: high numbers of species and traits in TRY make the two matrices large, but many cells in the matrices are empty. For this reason, I used "gap-filled" data provided by TRY (Kattge, personal communication, 22 July 2020), which was estimated by Bayesian hierarchical probabilistic matrix factorization (BHPMF) (Fazayeli et al. 2014; Schrodt 2015; Shan et al. 2012). In the TRY database, traits are grouped into eight main clusters: biodiversity, climate change, plant traits, functional diversity, carbon cycle, community, vegetation, and environmental filtering. Note that this cluster specification is unique to the TRY database and is not used here.

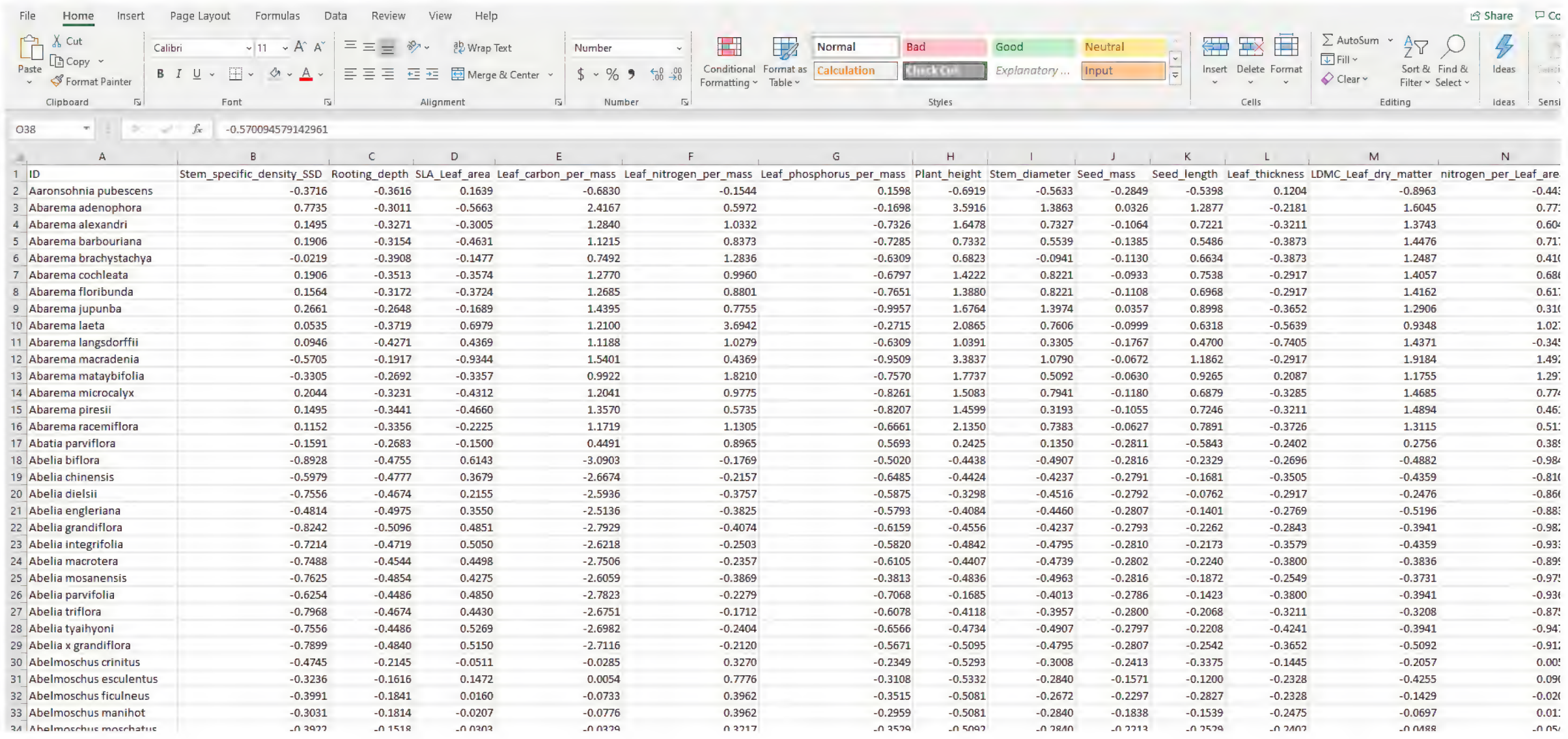
GIFT database (growth form data). GIFT integrates plant distributions, functional traits, phylogenetic information, and region-level geographic, environmental, and socio-economic data. It currently holds species lists for 2,893 regions across the globe, including about 315,000 taxonomically standardized species names and about 3 million species-by-region occurrences. In addition, GIFT contains information about the floristic status (native, endemic, alien, and naturalized) and takes advantage of the wealth of trait information in the regional Floras, complemented by data from global trait databases. Based on a hierarchical and taxonomical derivation scheme, GIFT holds information for 83 functional traits and more than 2.3 million trait-by-species combinations, and it achieves unprecedented coverage in categorical traits such as woodiness (~233,000 spp.) and growth form (~213,000 spp.).

IUCN "Red List" (protected status data). This classifies species at high risk of global extinction, each species categorized as follows: Not Evaluated, Data Deficient, Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, Extinct in the Wild, and Extinct. More than 120,000 species have been assessed (as of August 2020).

Jena experiment ("climber" status data). The Jena data was obtained through the TRY database with permission from the authors (Roscher et al. 2018). Many of the Jena traits overlapped with those from other databases, but one that did not (or at least with only a very few) was whether the plant was a "climber." Briefly, the "Jena experiment" was designed on a trait-based a priori definition of functional groups (grasses, legumes, small herbs, tall herbs), based on means, extent of variation (coefficient of variation across communities), and other metrics for nine functional traits (only one of which is used here, climber vs. non-climber).

Medicinal use data from public sources. This sample underestimates the number of plants with medicinal use, and this underestimation could be substantial. For example, even if it is likely that multiple species within a genus were used medicinally, the only species marked medicinal will be those that happen to be documented. Nonetheless, I opted to include this variable here, and specific sources are listed above. For example, Wikipedia.org (2020) lists *Achillea millefolium* (common yarrow) as a diaphoretic and stimulant (https://en.wikipedia.org/wiki/List_of_plants_used_in_herbalism); the European Medicines Agency (2020) lists *Echinacea angustifolia* (narrow-leaved coneflower) as an herb used to alleviate cough/cold symptoms (https://www.ema.europa.eu/sites/default/files/Medicines_output_herbal_medicines. xlsx), etc. If a plant was not listed on any "list" like the ones above, it was classified as "non-medicinal," which causes the unavoidable underestimation mentioned above.

Figure 1. Example of data used in this analysis, in Microsoft Excel (screenshot). Measures have been z-transformed, so units are standard deviations (not native units, such as millimeters).



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	A	B	C	D	E	F	G	H	I	J	K	L	M	N
1	ID	Stem_specific_density_SSD	Rooting_depth	SLA_Leaf_area	Leaf_carbon_per_mass	Leaf_nitrogen_per_mass	Leaf_phosphorus_per_mass	Plant_height	Stem_diameter	Seed_mass	Seed_length	Leaf_thickness	LDMC_Leaf_dry_matter	nitrogen_per_Leaf_are
2	Aaronsohnia pubescens	-0.3716	-0.3616	0.1639	-0.6830	-0.1544	0.1598	-0.6919	-0.5633	-0.2849	-0.5398	0.1204	-0.8963	-0.443
3	Abarema adenophora	0.7735	-0.3011	-0.5663	2.4167	0.5972	-0.1698	3.5916	1.3863	0.0326	1.2877	-0.2181	1.6045	0.77
4	Abarema alexandri	0.1495	-0.3271	-0.3005	1.2840	1.0332	-0.7326	1.6478	0.7327	-0.1064	0.7221	-0.3211	1.3743	0.60
5	Abarema barbouriana	0.1906	-0.3154	-0.4631	1.1215	0.8373	-0.7285	0.7332	0.5539	-0.1385	0.5486	-0.3873	1.4476	0.71
6	Abarema brachystachya	-0.0219	-0.3908	-0.1477	0.7492	1.2836	-0.6309	0.6823	-0.0941	-0.1130	0.6634	-0.3873	1.2487	0.41
7	Abarema cochleata	0.1906	-0.3513	-0.3574	1.2770	0.9960	-0.6797	1.4222	0.8221	-0.0933	0.7538	-0.2917	1.4057	0.68
8	Abarema floribunda	0.1564	-0.3172	-0.3724	1.2685	0.8801	-0.7651	1.3880	0.8221	-0.1108	0.6968	-0.2917	1.4162	0.61
9	Abarema jupunba	0.2661	-0.2648	-0.1689	1.4395	0.7755	-0.9957	1.6764	1.3974	0.0357	0.8998	-0.3652	1.2906	0.31
10	Abarema laeta	0.0535	-0.3719	0.6979	1.2100	3.6942	-0.2715	2.0865	0.7606	-0.0999	0.6318	-0.5639	0.9348	1.02
11	Abarema langsdorffii	0.0946	-0.4271	0.4369	1.1188	1.0279	-0.6309	1.0391	0.3305	-0.1767	0.4700	-0.7405	1.4371	-0.34
12	Abarema macradenia	-0.5705	-0.1917	-0.9344	1.5401	0.4369	-0.9509	3.3837	1.0790	-0.0672	1.1862	-0.2917	1.9184	1.49
13	Abarema mataybifolia	-0.3305	-0.2692	-0.3357	0.9922	1.8210	-0.7570	1.7737	0.5092	-0.0630	0.9265	0.2087	1.1755	1.29
14	Abarema microcalyx	0.2044	-0.3231	-0.4312	1.2041	0.9775	-0.8261	1.5083	0.7941	-0.1180	0.6879	-0.3285	1.4685	0.77
15	Abarema piresii	0.1495	-0.3441	-0.4660	1.3570	0.5735	-0.8207	1.4599	0.3193	-0.1055	0.7246	-0.3211	1.4894	0.46
16	Abarema racemiflora	0.1152	-0.3356	-0.2225	1.1719	1.1305	-0.6661	2.1350	0.7383	-0.0627	0.7891	-0.3726	1.3115	0.51
17	Abatia parviflora	-0.1591	-0.2683	-0.1500	0.4491	0.8965	0.5693	0.2425	0.1350	-0.2811	-0.5843	-0.2402	0.2756	0.38
18	Abelia biflora	-0.8928	-0.4755	0.6143	-3.0903	-0.1769	-0.5020	-0.4438	-0.4907	-0.2816	-0.2329	-0.2696	-0.4882	-0.98
19	Abelia chinensis	-0.5979	-0.4777	0.3679	-2.6674	-0.2157	-0.6485	-0.4424	-0.4237	-0.2791	-0.1681	-0.3505	-0.4359	-0.81
20	Abelia dielsii	-0.7556	-0.4674	0.2155	-2.5936	-0.3757	-0.5875	-0.3298	-0.4516	-0.2792	-0.0762	-0.2917	-0.2476	-0.86
21	Abelia engleriana	-0.4814	-0.4975	0.3550	-2.5136	-0.3825	-0.5793	-0.4084	-0.4460	-0.2807	-0.1401	-0.2769	-0.5196	-0.88
22	Abelia grandiflora	-0.8242	-0.5096	0.4851	-2.7929	-0.4074	-0.6159	-0.4556	-0.4237	-0.2793	-0.2262	-0.2843	-0.3941	-0.98
23	Abelia integrifolia	-0.7214	-0.4719	0.5050	-2.6218	-0.2503	-0.5820	-0.4842	-0.4795	-0.2810	-0.2173	-0.3579	-0.4359	-0.93
24	Abelia macrotera	-0.7488	-0.4544	0.4498	-2.7506	-0.2357	-0.6105	-0.4407	-0.4739	-0.2802	-0.2240	-0.3800	-0.3836	-0.89
25	Abelia mosanensis	-0.7625	-0.4854	0.4275	-2.6059	-0.3869	-0.3813	-0.4836	-0.4963	-0.2816	-0.1872	-0.2549	-0.3731	-0.97
26	Abelia parvifolia	-0.6254	-0.4486	0.4850	-2.7823	-0.2279	-0.7068	-0.1685	-0.4013	-0.2786	-0.1423	-0.3800	-0.3941	-0.93
27	Abelia triflora	-0.7968	-0.4674	0.4430	-2.6751	-0.1712	-0.6078	-0.4118	-0.3957	-0.2800	-0.2068	-0.3211	-0.3208	-0.87
28	Abelia tyaihyoni	-0.7556	-0.4486	0.5269	-2.6982	-0.2404	-0.6566	-0.4734	-0.4907	-0.2797	-0.2208	-0.4241	-0.3941	-0.94
29	Abelia x grandiflora	-0.7899	-0.4840	0.5150	-2.7116	-0.2120	-0.5671	-0.5095	-0.4795	-0.2807	-0.2542	-0.3652	-0.5092	-0.91
30	Abelmoschus crinitus	-0.4745	-0.2145	-0.0511	-0.0285	0.3270	-0.2349	-0.5293	-0.3008	-0.2413	-0.3375	-0.1445	-0.2057	0.00
31	Abelmoschus esculentus	-0.3236	-0.1616	0.1472	0.0054	0.7776	-0.3108	-0.5332	-0.2840	-0.1571	-0.1200	-0.2328	-0.4255	0.09
32	Abelmoschus ficulneus	-0.3991	-0.1841	0.0160	-0.0733	0.3962	-0.3515	-0.5081	-0.2672	-0.2297	-0.2827	-0.2328	-0.1429	-0.02
33	Abelmoschus manihot	-0.3031	-0.1814	-0.0207	-0.0776	0.3962	-0.2959	-0.5081	-0.2840	-0.1838	-0.1539	-0.2475	-0.0697	0.01
34	Abelmoschus moschatus	-0.3922	-0.1518	-0.0303	-0.0329	0.3217	-0.3529	-0.5092	-0.2840	-0.2213	-0.2529	-0.2402	-0.0488	-0.05

Statistical Analysis

General Approach. All the data sets listed above have a column in common — i.e., species name ("Genus species") — which allowed the data sets to be linked into a single matrix. Figure 1 shows a screenshot of a portion of the data open in Microsoft Excel, where each row is a species and each column is a trait (e.g. seed length). Many unsupervised machine learning algorithms (not used here) attempt to group the rows — e.g., since each row is a species, perhaps the algorithm will try to group species into genera. By contrast, the goal in the present paper was to group the columns (traits). The purpose of grouping columns is discussed below, but the idea is that the columns relate to each other (e.g. seed mass correlates with plant height). Another benefit of clustering columns is that each species then receives a score for each cluster; for example, if traits 1, 2, and 3 cluster to form Variable Cluster 1, each plant will receive a score for Variable Cluster 1 that is on the same scale as all other species' scores (and therefore comparable to them). These scores can then be used in subsequent analyses, whether genetic or otherwise (e.g., using trait scores to predict crop viability).

Missing data imputation. When the data matrices described above were merged by species, this introduced gaps into the data, because some species will have data for only some of the data types. For example, *Aaronsohnia pubescens* has complete data from the main TRY database but is missing data on growth form. To fill these gaps, I first excluded any species missing from the main TRY database ("TRY database" above), which left N=52,104 species. Of these, most (87%) had at least one missing value from the remaining data sets (growth form from the GIFT database, etc.). Missing data were imputed using the random forest algorithm (Svetnik et al. 2003) in the *missForest* package (Stekhoven 2013).

Bivariate (1-on-1) relationships. I first estimated the correlations among traits, and because the traits are a mix of continuous and categorical (yes/no) variables, the result is a mixed correlation matrix. That is, correlations between continuous variables are standard Pearson correlations, correlations between categorical variables are tetrachoric, and correlations between continuous and categorical variables are biserial[2]. All three correlation types (Pearson, tetrachoric, and biserial) are on the same scale and span the full theoretical range from -1 to 1 (unlike point-biserial correlations, for example).

Exploratory Factor Analysis (EFA). The above correlation matrix was used as input for exploratory factor analysis (Gorsuch 1983; Kim & Mueller 1978a, 1978b), where the term "factor" is equivalent to the term "Variable Cluster" used above in the "General Approach" subsection. The number of factors was determined by subjective examination of the scree plot, which clearly suggested three factors. For thoroughness I also estimated the appropriate number of factors using many conventional methods: Cattell-Nelson-Gorsuch (Gorsuch & Nelson 1981), multiple regression (Zoski & Jurs 1993), optimal coordinate (Raiche et al. 2013), acceleration factor (Raiche et al. 2013), Bartlett index (Bartlett 1950), Bentler-Yuan index (Bentler & Yuan 1998), and the minimum Bayesian Information Criterion (Schwarz 1978). These methods suggest 3, 4, 7, 7, >20, >20, and >20 factors, respectively. Nonetheless, the scree plot is clear in suggesting three factors, so in the interest of parsimony, I opted for that as the final number.

With the number of factors decided, it's necessary to choose a rotation. Because I did not necessarily expect simple structure (Thurstone 1947) — i.e., I did not believe *a priori* that each phenotype would load on one and only one factor — iterated target rotation (ITR) was employed (Moore 2013; Moore et al. 2015), which is more likely to detect complex structure (cross-loadings) than are traditional simple structure rotations such as oblimin or promax. Specifics of ITR are beyond the present scope, but the idea is to start with a conventional simple structure rotation (here, promax)

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[2] Note that these are biserial, not point-biserial. See Kemery, Dunlap, & Griffeth (1988) for details.

and use that rotated solution (pattern matrix) to construct a partially-specified[3] target matrix for use in a subsequent target rotation. This subsequent target-rotated solution is then used in the same way as the analytic rotation was first used, to build another target matrix. This third target-rotated solution is used to build another target, and so on, until a constructed target matches one that was previously used in the sequence, indicating algorithm convergence. Note that target matrices created in the above sequence are not limited to one estimated element per row — a configuration that would correspond with simple structure — but rather are specified to allow whatever level of complexity is suggested by the previous solution in the target-iteration sequence. Indeed, if a solution includes a row with salient (> 0.20) loadings on all factors, the resulting target would be completely unspecified for that row (allowing free estimation of all elements in that row). The opposite — all row elements specified as zero — is also possible.

Quasi-Confirmatory[4] Factor Analysis (CFA). The final ITR solution was used to construct and estimate a Bayesian CFA. The first step of the CFA was to decide how to model the multidimensionality. In any multidimensional factor model, the multiple factors will undoubtedly correlate with each other, and there are three ways to model this phenomenon (see Reise, Moore, & Haviland 2010, Figure 1).

1) Simply allow the factors to correlate. This is called a "correlated traits" model, and there is no "overall" factor in common among all traits. If I had several measurements of airplanes and factor analyzed them, I might find that there was a factor clearly related to wing size (wing length, wing width, wing deadweight, etc.) and another factor related to capacity (number of seats, number of cargo holds, fuselage diameter, etc.), among others. In this scenario, a correlated-traits model makes sense because airplane capacity and wing size are correlated out of physical necessity. More load requires more aerodynamic surface area and possibly more engines, which are usually held by the wings. So, they correlate; end of story.

2) Suppose the inter-factor correlation is caused by a higher-level phenomenon influencing both factors; this is called a "higher-order" (or "second-order") model. If I factor analyzed several measurements of adult athletes, I might find a factor related to basketball ability (total points per game, number of rebounds, etc.) and another related to food (weekly sugar intake, weekly niacin intake, etc.), among others. Here, there is a clear reason these two factors would correlate: total body mass. An athlete's size influences both his/her ability at basketball and his/her nutritional intake, making "size" the higher-order factor in this case.

3) Suppose the inter-factor correlation is caused by a higher-level phenomenon directly influencing all traits, which are themselves also influenced by factors unique to them. This is called a "bifactor" model (Reise 2012; Holzinger & Swineford 1937) because all variables are influenced by two phenomena simultaneously: a "general" factor causing all inter-variable correlations, and a "specific" factor causing inter-variable correlations only among variables that cluster together. If I had question responses (correct/incorrect) to a test of human cognitive abilities, I might find a factor related to memory (episodic memory, list memorization, etc.) and one related to complex reasoning (progressive matrices, verbal analogies, etc.), among others. All of these tests would correlate because of the well-documented "g" factor of human intelligence, affecting all test responses of any kind. Thus, it makes sense to have a general factor directly influencing all tests (episodic memory, progressive matrices, etc.) rather than having a higher-order factor that influences the latent phenomena of memory and complex reasoning. In addition to the general factor, however, there will undoubtedly be some unique influence of the specific abilities of

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[3] Partially-specified targets include only two types of elements: either "0", indicating that the rotation should "try" to get that element as close to 0 as possible, or "?" (unspecified), indicating that the rotation should freely estimate that element.

[4] "Quasi-" because there is no real, cross-validated confirmation here.

memory and complex reasoning causing the tests to correlate slightly more strongly with tests in the same cluster (memory or complex) than with all tests in general. Specific factors are therefore needed to account for said unique influence. Importantly, when the general factor is modeled as in the bifactor, there is no need to allow the specific factors to correlate. The bifactor model is therefore orthogonal.

Here, I model plant traits as a bifactor model (#3 above) for two main reasons. First, if there is a "general" factor influencing all plant phenotypes, I want to know the extent to which that general factor influences some specific traits more than others. In a higher-order model (#2 above), there would be no direct relationships between the general factor and the traits. All relationships have to be "routed" through the lower-level factors, meaning that if two traits belong to the same sub-factor (e.g., leaf size) there is no way to determine whether one traits (e.g. leaf dry mass) relates more strongly to the general factor than does another (e.g. leaf width) except to multiply their loadings by each other, in which case there is a built-in constraint whereby both traits' loadings must be multiplied by the same higher-order loading. The bifactor model does not have this constraint, called a "proportionality constraint." The second reason I use a bifactor model is that I wish to produce phenotype factor scores for public use, and one of the most convenient features of bifactor scores is that they are orthogonal (independent), allowing them to be used simultaneously as predictors in a statistical model without having to worry about collinearity. Note that a bifactor model is the only way[5] to sensibly model correlated phenomena as though they were independent. The above bifactor model was used to generate orthogonal phenotype scores for public use.

RESULTS

Table 1 shows the unidimensional, 2- and 3-factor exploratory solutions, plus the Bayesian-estimated quasi-CFA. The unidimensional model is determined most strongly by terrestrial status, plant height, and leaf dry mass. The forb and herb growth form variables also have moderate negative loadings on the unidimensional model, suggesting this model essentially captures "tree-ness" or a contrast factor between "treeness" and "herbness." The two-factor model in Table 1 shows us what happens when the traits are allowed to dissociate into two groups: they separate into one factor dominated by leaf size, and a second factor dominated by leaf dry matter content, probability of being in the Australasian realm, and (inversely) specific leaf area. The three-factor model comprises two factors virtually identical to the two factors above, with a third factor dominated by wood fiber and vessel lengths. Finally, the three rightmost columns in Table 1 (highlighted yellow) show the Bayesian model from which scores were generated. The results are similar enough to the three-factor exploratory model to not warrant further description, but note again that the correlated-traits scores corresponding to the "Bayes 3-Factor" model in Table 1 are included in the score release and can be assumed just as valid as the bifactor scores.

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[5] It is easy to overlook the difficulty of this problem — i.e. trying to produce orthogonal scores from phenomena that are correlated. Using an orthogonal rotation (e.g. varimax) does not accomplish the task, because orthogonal rotations force orthogonality where there is none. For example, there simply is no such thing as psychosis independent of anxiety, genetic risk independent of ancestry, verbal ability independent of quantitative ability, etc., so if a model has produced these things orthogonal to one another, then whatever those things are, they are not the phenomena one set out to measure. The bifactor model solves the problem by including an additional factor (the "general") to account for the inter-factor correlations. Orthogonality is therefore not forced on the solution, but rather follows from the specific factors' competing with the general factor for variance explained in each individual phenotype.

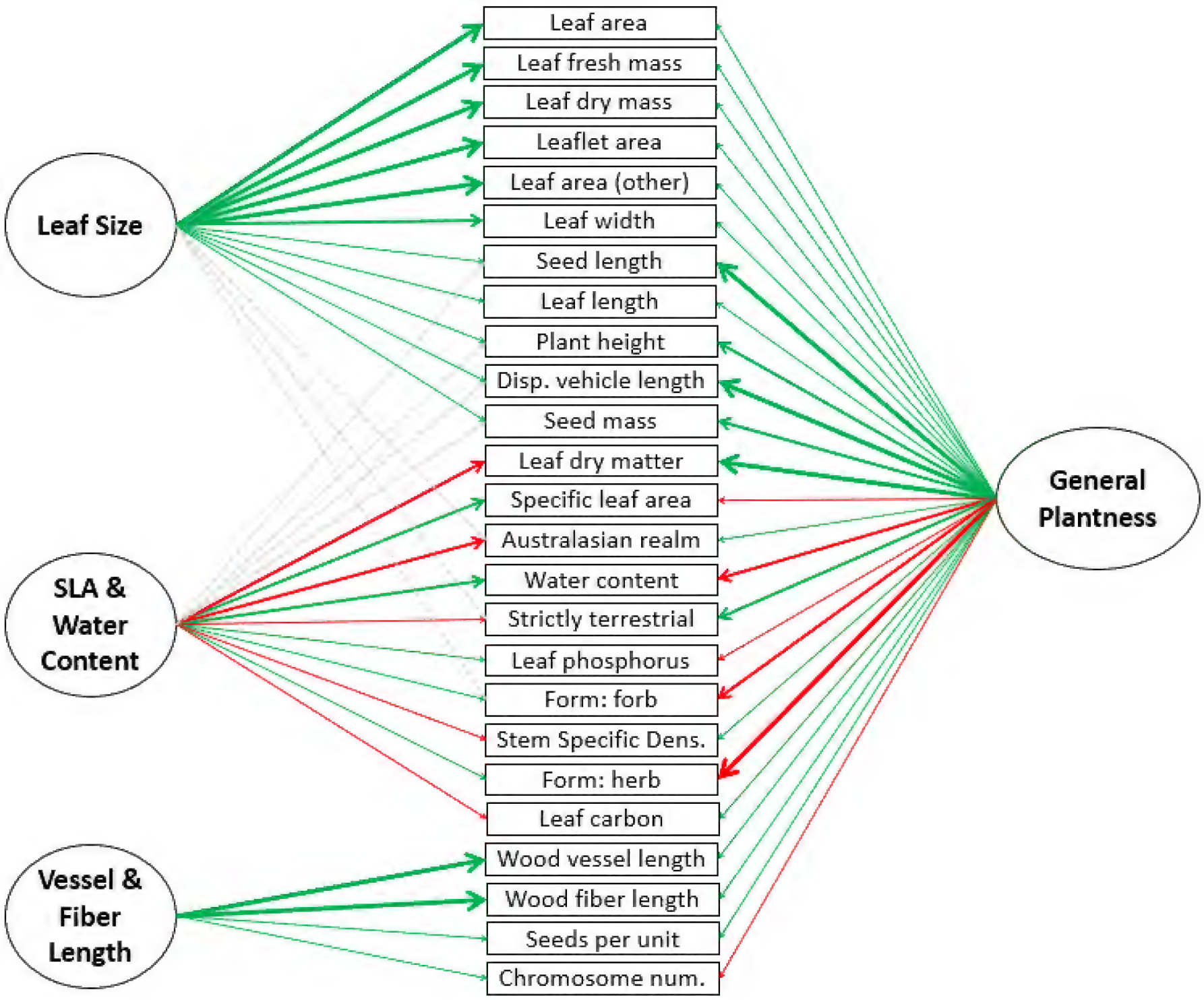

Figure 2. Path diagram showing the bifactor measurement model. Note. Exact loadings can be found in Table 2; items with very low communalities have been removed from the diagram for ease of visualization but were not removed before score-creation; green indicates positive loading (association); red indicates negative loading; thickest lines represent loadings with absolute value > 0.70; second-thickest lines represent loadings with absolute value 0.50-0.70; thinnest lines represent all other loadings (even those < 0.01); dotted lines indicate cross-loadings (complex structure); direction of arrows (from factors to traits) is consistent with the latent trait theory (factor analysis) whereby the latent factors cause the traits, itself consistent with the idea that genes cause traits.

Table 2 shows the results of the bifactor model using the same item-factor configuration suggested by the exploratory models above but with the addition of a General Factor of Plantness. **Factor 1** is Leaf Size, determined most strongly by dry and fresh leaf mass. **Factor 2** is SLA/Water Content (specific leaf area and water content), indicated most strongly by leaf water content and the inverse of leaf dry matter content. **Factor 3** is Vessel/Fiber Length. Finally, the factor of **General Plantness** (leftmost column in Table 2 and right side of Figure 2) is most strongly indicated by greater seed length, greater seed mass, greater dispersal vehicle length, greater plant height, greater leaf dry matter content, lower water content per leaf mass, greater probability of being a tree or shrub, and greater probability of a strictly terrestrial habit. As with the unidimensional model described in the paragraph above, the General Factor of Plantness is definitely aligned with "treeness," but note the

difference in emphasis on terrestrial status and plant height (for the unidimensional[6]) versus dry matter content and seed size (for bifactor General Plantness). Figure 2 shows the bifactor model in the traditional way, via a path diagram, but with strengths of associations represented graphically (by color and line thickness) rather than by numerical coefficients (available in Table 2).

Figures 3-6 show the frequencies (histograms) of the four factor scores generated from the bifactor model in Table 2. All, including examples, make intuitive sense although interpretation of the General Plantness factor is risky at this stage.

Figure 7 shows the bivariate relationships among factor scores from both the correlated-traits model and the bifactor model. The specific bifactor factors for leaf size and Fiber/Vessel Length are highly correlated with the equivalent scores from the correlated-traits model (correlations 0.90+). Also of note, the general bifactor factor correlated 0.81 with the water content factor from the correlated-traits model. This provides a hint that the General Plantness factor is some combination of water content (or lack thereof), plant height, and possibly tree form, among others.

Figures 8-13 show scatterplots of a few selected species (mix of famous, common, and scientifically important) plotted with respect to two dimensions at a time (e.g. Leaf Size and General Plantness). The diagonal dotted line is the identity line (y = x), and while the scatters appear to show some positive or negative correlations, all data viewed together does not show such patterns (see Figure 7, where the only clear correlations are between equivalent corr-traits//bifactors scores, never between bifactor//bifactor scores). Indeed, if all species were plotted together in Figures 6-11, there would be no clear relationship at all—simply a cloud of points—which is one of the strengths of the bifactor model. When developing scores for use in secondary analyses, it is best if those scores are uncorrelated.

Table 1. Unidimensional, 2-factor, and 3-factor exploratory solutions for the TRY+ Database, with 3-factor quasi-confirmatory solution.

		Exploratory 2-Factor		Exploratory 3-Factor			Bayes 3-Factor		
Variable (trait)	Uni	F1	F2	F1	F2	F3	F1	F2	F3
Leaf_area	0.68	0.87		0.88			0.92		
Leaf_fresh_mass	0.67	0.86		0.84			0.97		
Leaf_dry_mass	0.78	0.83		0.82			0.96		
Leaflet_area	0.60	0.81		0.82			0.83		
other_leaf_area	0.62	0.80		0.78			0.80		
Leaf_width	0.59	0.76		0.76			0.74		
Seed_length	0.77	0.47	0.52	0.53	0.45		0.39	0.44	
Leaf_length	0.41	0.58		0.52			0.54		
Plant_height	0.80	0.48	0.57	0.52	0.50		0.42	0.46	
Disp_vehicle_length	0.69	0.42	0.48	0.48	0.40		0.35	0.41	
Neotropical_realm	0.53	0.43		0.48			0.42		
Seed_mass	0.56	0.35	0.37	0.40	0.31		0.31	0.27	

[6] It is tempting to view the unidimensional model as "General Plantness" just like we're viewing the bifactor general factor. However, unidimensional models estimated in multidimensional data (as here) yield biased loadings (Reise, Moore, & Maydeu-Olivares, 2011; Reise, Cook, & Moore, 2015). Correct loadings on the general factor can be identified only by estimating the multidimensional group factors along with it (in a full bifactor model, as here).

N_isotope_signature_Leaf	0.25	0.27		0.31			0.21		
climber	0.05	0.14		0.18			0.06		
LDMC_Leaf_dry_matter	0.57		0.84		0.84			0.93	
SLA_Leaf_area	-0.35		-0.71		-0.78			-0.66	
Australasian_realm	0.19	-0.44	0.72	-0.44	0.76		-0.25	0.65	
water_content_per_leaf_mass	-0.48		-0.71		-0.71			-0.84	
strictly_terrestrial	0.87	0.47	0.68	0.50	0.61		0.40	0.45	
Leaf_phosphorus_per_mass	-0.35		-0.57		-0.60			-0.52	
form_Forb	-0.56		-0.60		-0.59			-0.55	
Stem_specific_density_SSD	0.38		0.60		0.59			0.53	
form_Herb	-0.66		-0.59	-0.34	-0.53		-0.25	-0.53	
Leaf_carbon_per_mass	0.39		0.47		0.49			0.47	
Leaf_nitrogen_per_mass	-0.13		-0.40	0.31	-0.49		0.10	-0.41	
nitrogen_per_Leaf_area	0.27		0.45		0.48			0.41	
Stem_diameter	0.48		0.44		0.45			0.37	
Rooting_depth	0.41		0.39		0.36			0.34	
form_Shrub_or_SubShrub	-0.03	-0.35	0.31	-0.34	0.34		-0.32	0.26	
Specific_root_length_SRL	-0.29		-0.36		-0.34			-0.34	
endangered_or_worse	0.25		0.28		0.29			0.27	
Nearctic_realm	-0.28		-0.23		-0.20			-0.13	
documented_medicinal	0.00		-0.13		-0.15			-0.11	
Wood_vessel_length	0.17	0.33				0.85			0.98
Wood_fiber_lengths	0.38	0.41				0.63			0.75
Seed_number_per_unit	0.07	0.15				0.48			0.48
chromosome_number	-0.08		-0.24			0.46			0.45
Stem_conduit_density	-0.27		-0.22			0.37			0.25
cpDNA_content	-0.10		-0.15			0.36			0.33
Leaf_thickness	-0.04	-0.16				0.33			0.16
Stem_conduit_diameter	0.23	0.34				0.32			0.39
Seed_germination_rate	-0.13	-0.12				-0.24			-0.17

Table 2. Quasi-confirmatory bifactor solution for the TRY+ Database, with three specific factors and one general (overall) factor.

Variable	Gen	F1	F2	F3
Leaf_area	0.33	0.85		
Leaf_fresh_mass	0.29	0.94		
Leaf_dry_mass	0.42	0.87		
Leaflet_area	0.25	0.79		
other_leaf_area	0.25	0.76		
Leaf_width	0.28	0.67		

Seed_length	**0.92**	0.06	-0.40	
Leaf_length	0.21	0.49		
Plant_height	**0.68**	0.25	-0.01	
Disp_vehicle_length	**0.83**	0.05	-0.35	
Neotropical_realm	0.35	0.30		
Seed_mass	**0.64**	0.06	-0.35	
N_isotope_signature_Leaf	0.20	0.13		
climber	0.02	0.05		
LDMC_Leaf_dry_matter	**0.73**		0.60	
SLA_Leaf_area	-0.45		-0.50	
Australasian_realm	0.40	-0.14	0.51	
water_content_per_leaf_mass	**-0.63**		-0.61	
strictly_terrestrial	**0.68**	0.25	0.02	
Leaf_phosphorus_per_mass	-0.38		-0.37	
form_Forb	-0.57		-0.17	
Stem_specific_density_SSD	0.42		0.30	
form_Herb	**-0.70**	-0.13	-0.06	
Leaf_carbon_per_mass	0.43		0.19	
Leaf_nitrogen_per_mass	-0.21	0.04	-0.36	
nitrogen_per_Leaf_area	0.27		0.31	
Stem_diameter	0.35		0.12	
Rooting_depth	0.35		0.08	
form_Shrub_or_SubShrub	-0.03	-0.19	0.34	
Specific_root_length_SRL	-0.33		-0.12	
endangered_or_worse	0.25		0.06	
Nearctic_realm	-0.14		-0.03	
documented_medicinal	-0.03		-0.14	
Wood_vessel_length	0.05			0.96
Wood_fiber_lengths	0.32			0.74
Seed_number_per_unit	0.00			0.49
chromosome_number	-0.20			0.48
Stem_conduit_density	-0.27			0.26
cDNA_content	-0.08			0.34
Leaf_thickness	-0.10			0.17
Stem_conduit_diameter	0.12			0.39
Seed_germination_rate	-0.08			-0.19

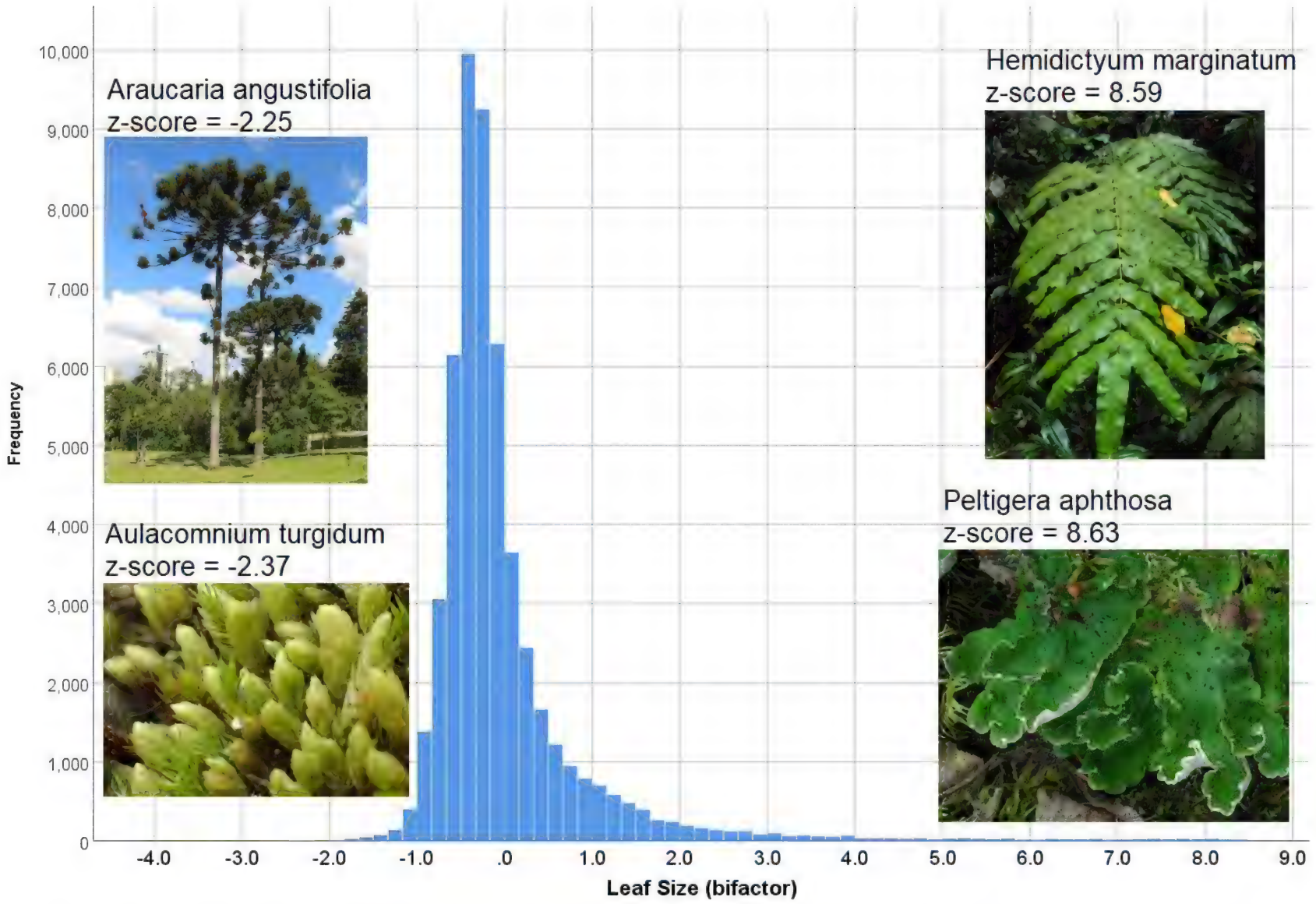

Figure 3. Histogram of Leaf Size factor score from the bifactor model, with extreme examples.

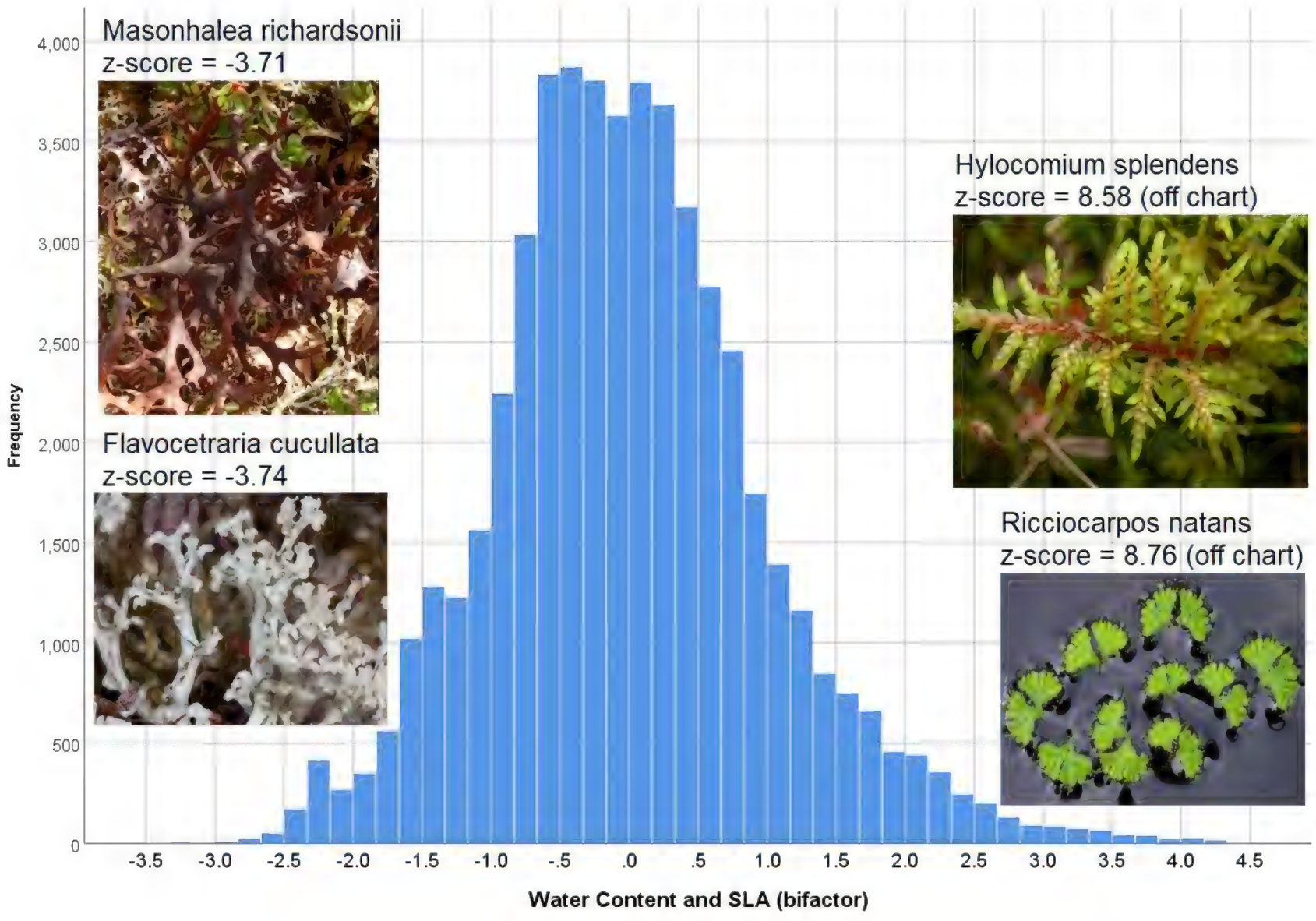

Figure 4. Histogram of Water Content and SLA (specific leaf area) factor score from the bifactor model, with extreme examples.

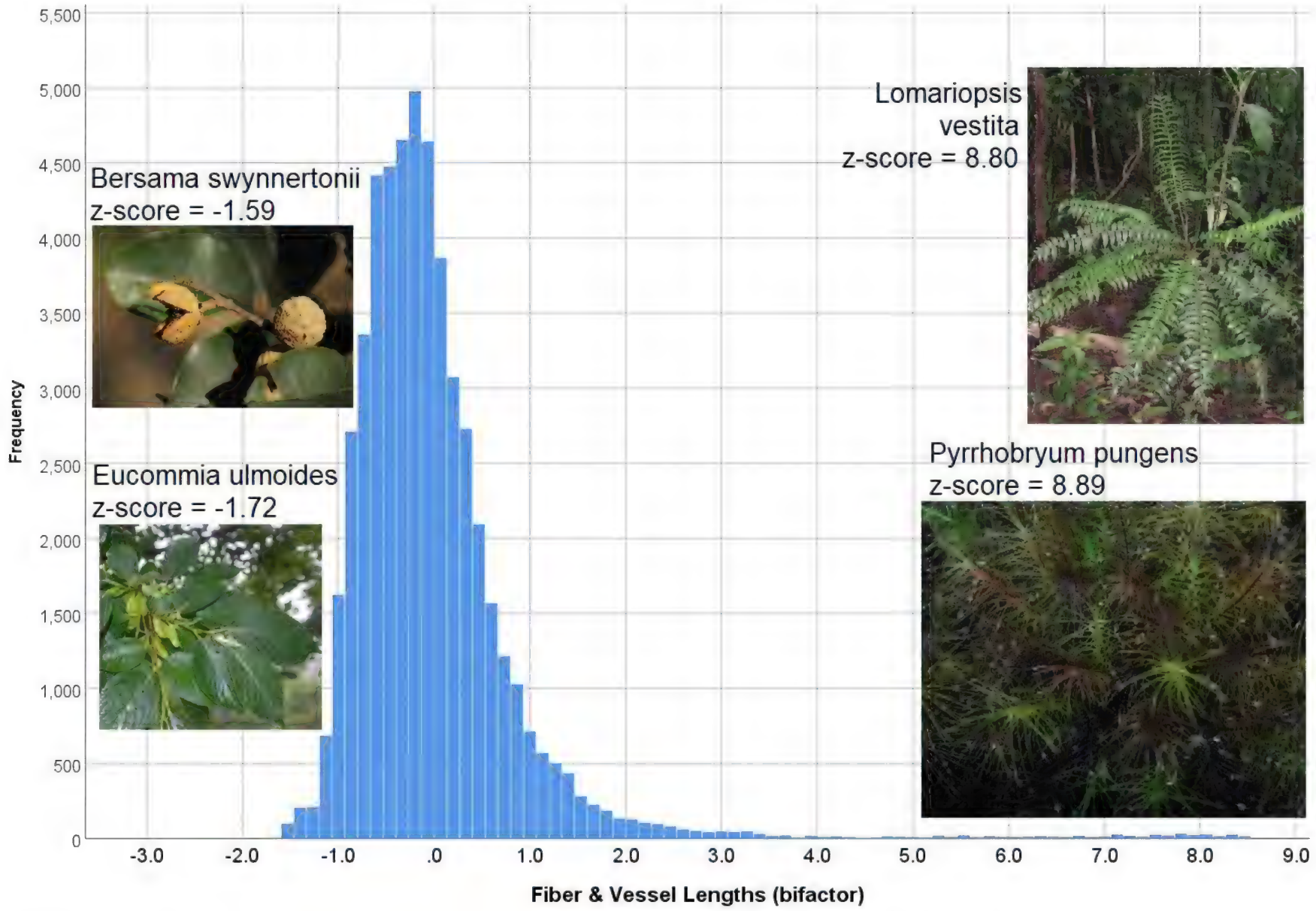

Figure 5. Histogram of Vessel/Fiber Lengths score from the bifactor model, with extreme examples.

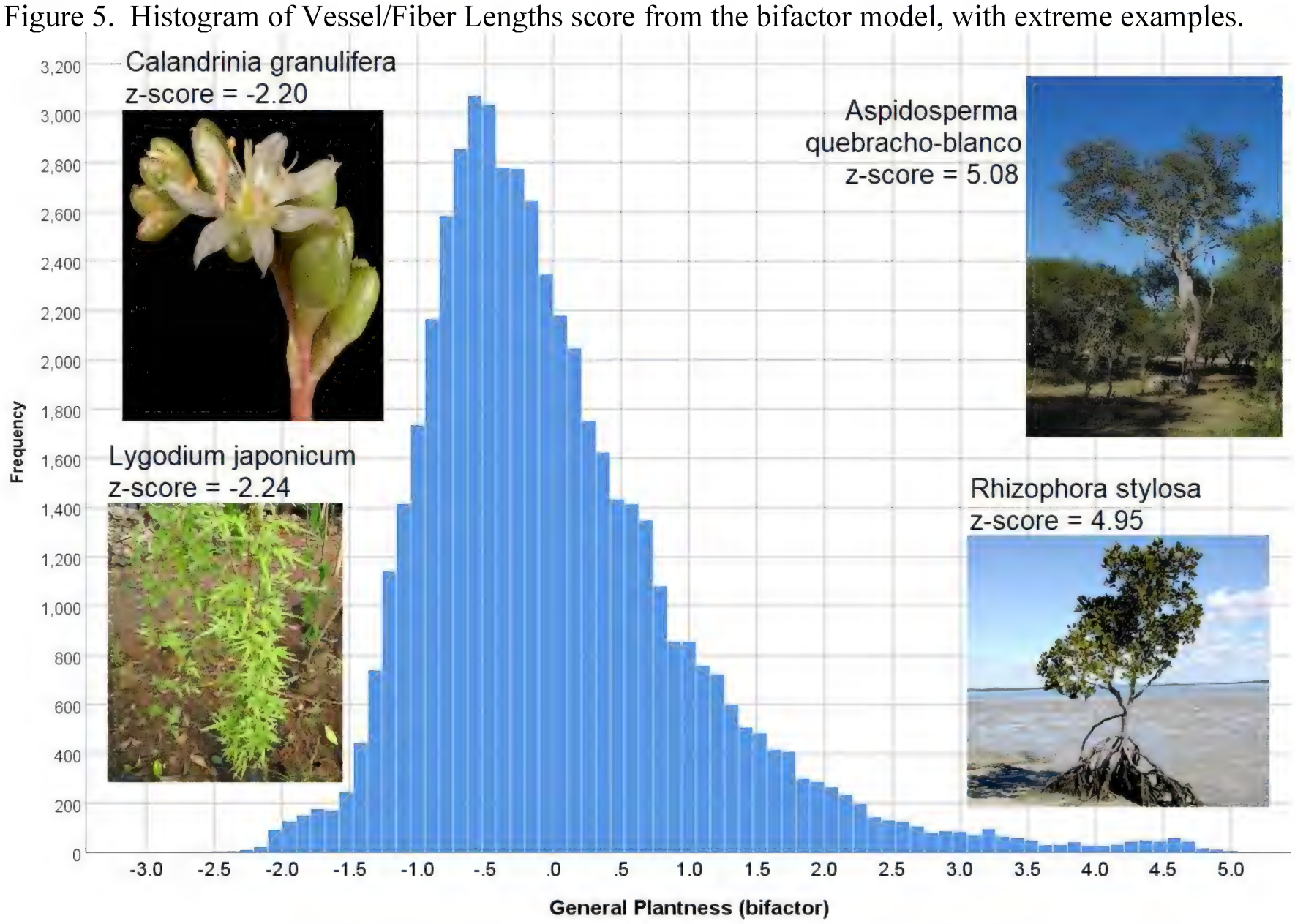

Figure 6. Histogram of General Plantness score from the bifactor model, with extreme examples.

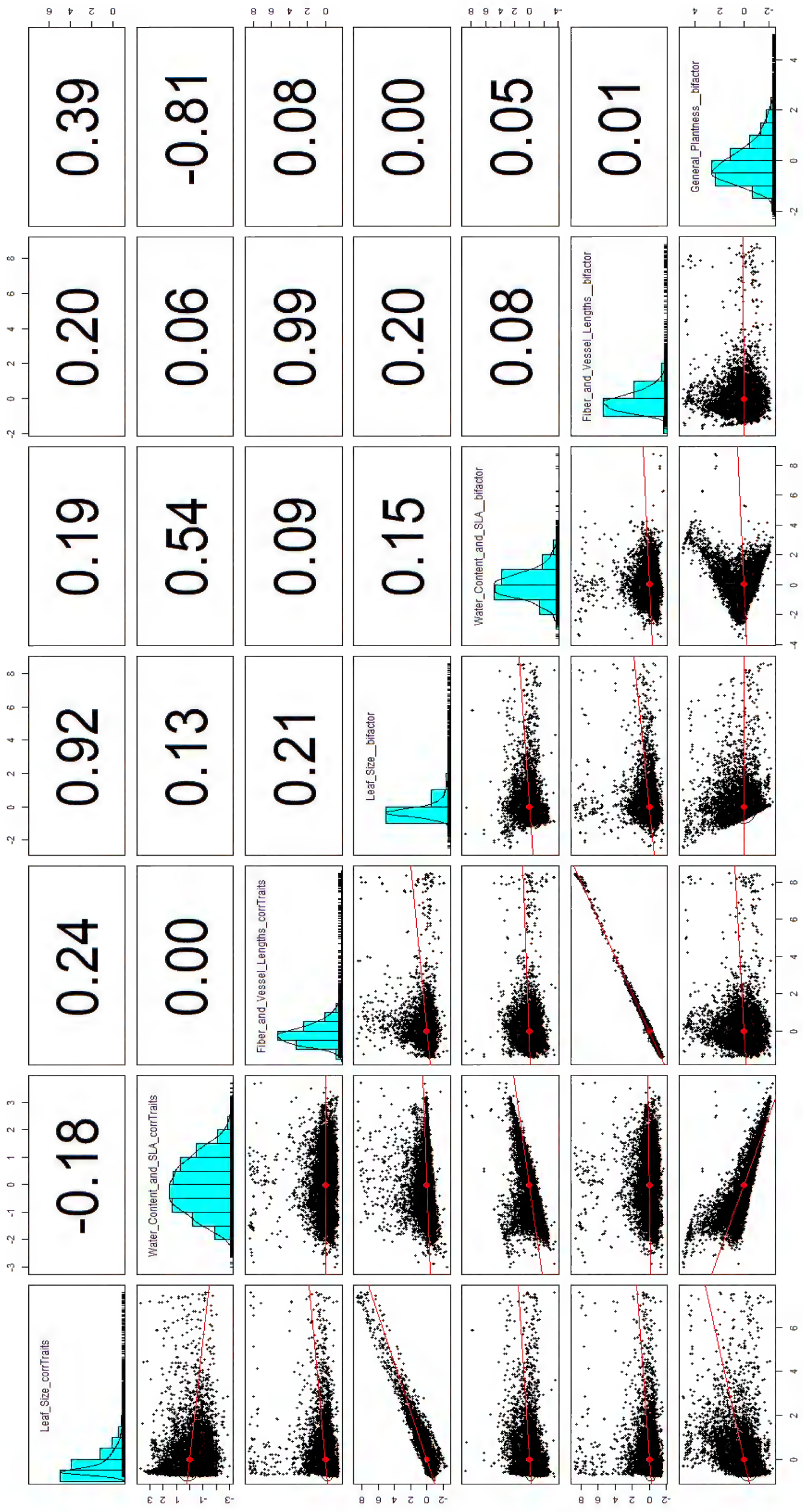

Figure 7. Correlations among plant factor scores from the correlated-traits and bifactor models.

DISCUSSION

The current study adds to the methodological and plant trait literature in two ways. First, I present the bifactor model as a possible solution to the problem of inter-factor collinearity, a problem not solved by any existing orthogonalization method. Second, I allow complex structure (cross-loadings) at the exploratory phase, allowing a model that more closely represents the sample (albeit at a cost to parsimony). The latter contribution, use of iterated target rotation, is quite novel and may grow to replace existing simple structure rotations if detection of complex structure (as here) proves useful. The fact that ITR will detect simple structure as well as complex structure—i.e., if ITR is overkill, it will return a simple structure solution—is all the more reason to expect the shift away from rotations that force simple structure. The bifactor model, likewise, introduces the idea of a single factor/dimension underlying all plant traits, which, if supported through genetic studies, will provide another dimensional trait score for use in prediction studies (e.g. predicting crop yields or any other plant-related outcome). From the botany perspective, the most important output from this project is the set of factor scores for use in subsequent studies. These scores likely differ from existing plant trait scores in that (1) they are orthogonal, and (2) they include a General Factor of Plantness.

The current study has some notable limitations. First, analyses were entirely exploratory, leaving for later studies investigation of the veracity of the measurement model arrived at through exploration. A more common pipeline for development of measurement models is to conduct exploratory analyses in one random portion of the sample and then *test* the model(s) in the other (non-overlapping) portion of the sample. I made the judgment call here that the exploratory models alone are enough for the present report, and I intend to investigate the reproducibility of the models in the same sample (analogous to the pipeline above) using bootstrapping. Nonetheless, even after this second study, it will have been done only in this sample. A true test of the measurement model presented here will be in a new sample — i.e., because there is natural variation within species, it would be optimal to collect more specimens of the same species used here and re-run these analyses. More realistically, these analyses should be redone after the TRY database has been expanded (as it constantly will be). This would add not only more specimens of the same species, but more species overall. A second limitation of the present study is that the imputation of missing data for growth form, region, endangeredness, medicinal use, and climber status was done without consideration of the multilevel (clustered) nature of the data — i.e., species within genera within families, etc. Clustering and other multilevel structure affects standard errors more than point estimates (Peugh 2005; see Equation 5), so the hope is that ignoring the nesting will increase only error, not bias. However, this "hope" could be tested by future researchers by comparing random forest imputation to an imputation method that considered the nested data structure (e.g. BHPMF mentioned above; also see Moreno-Martinez et al. 2018). Third, given the novelty of the present problem (does General Plantness "exist"?), it is possible that use of iterated target rotation complicates the problem unnecessarily at this early stage. I suggest that the approach used here — i.e., if there is any reason to doubt simple structure, use ITR — is best practice, but future researchers should examine simple structure rotations of these solutions, nonetheless. Indeed, the small-to-moderate cross loadings in Table 2 (only one reaching absolute value = 0.40) hint that ITR might not be necessary. Finally, I had to make many "executive decisions" while collecting, merging, and analyzing these data, and the decisions could not all feasibly be documented. Examples include decisions about whether to delete (versus manually correct) ambiguously misspelled species names, whether to distinguish among variations and subspecies in the analyses (decision was no on both counts), how to aggregate across multiple samples of the same species (decision was to take the mean), and dozens more. Documentation was foregone in some cases simply for the sake of speed, and any study performed by an individual in this way should be viewed with caution and replicated by a team, if possible.

This paper addresses an important methodological issue related to the bifactor model, which is the question of whether it makes sense to estimate one even when the correlated-traits model provides no evidence for a general factor. Shilton et al. (under review) provide some evidence for the potential utility

of bifactor models even when preliminary analyses might suggest that a hierarchical approach like the bifactor is unnecessary. They take a correlated-traits model presented in Moore et al. (2020) and apply a bifactor model (in a different data set) even though the inter-factor correlations from the models in Moore et al. were quite weak. Unsurprisingly, the general factor in Shilton's bifactor model is determined by a mixture of items across group factors, with item loadings on the general factor varying substantially across and *within* group factor. This in itself provides no evidence for or against a bifactor model necessarily, but it does suggest that if there is a general factor underlying item responses to some extent, it would not be noticeable in the correlated-traits (or higher-order) models. Most importantly, Shilton et al. found that the general factor score from the bifactor model had better criterion validity than any other score in the model. This provides one piece of evidence in favor of "trying" bifactor models even when inter-factor correlations suggest there is no general factor (obviating a bifactor model). If it turns out that no items have strong loadings on the general factor, then the researcher will know that the original hint (weak inter-factor correlations) was correct. On the other hand, if some specific items within the group factors have strong loadings on the general factor, the above study suggests that the general factor score might be a valid metric. In the present study, the question remains, is the General Factor of Plantness a valid measure of something interesting or useful (as turned out in the Shilton et al. study)? Further research is needed, but I speculate that the answer is yes, "General Plantness" is interesting and useful and the corroborating evidence for its existence will come (or already is available) from genetics.

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ELECTRONIC MATERIAL

Factor scores are available for download at <https://www.mooremetrics.com/wp-content/uploads/2020/08/Plant_Factor_Scores.csv>. Note that scores ending in "__bifactor" are the bifactor scores used here. Scores ending in "__corrTraits" are generated from a model that does not include a general factor (i.e. a correlated-traits model). The .r file for conducting iterated target rotation, along with the Mplus files for conducting the Bayesian CFAs are available at <http://www.mooremetrics.com/wp-content/uploads/2020/08/Iterated_Target_Rotation_and_Mplus_scripts.zip>. All files and figures are available at <https://mooremetrics.com/3fp/>.

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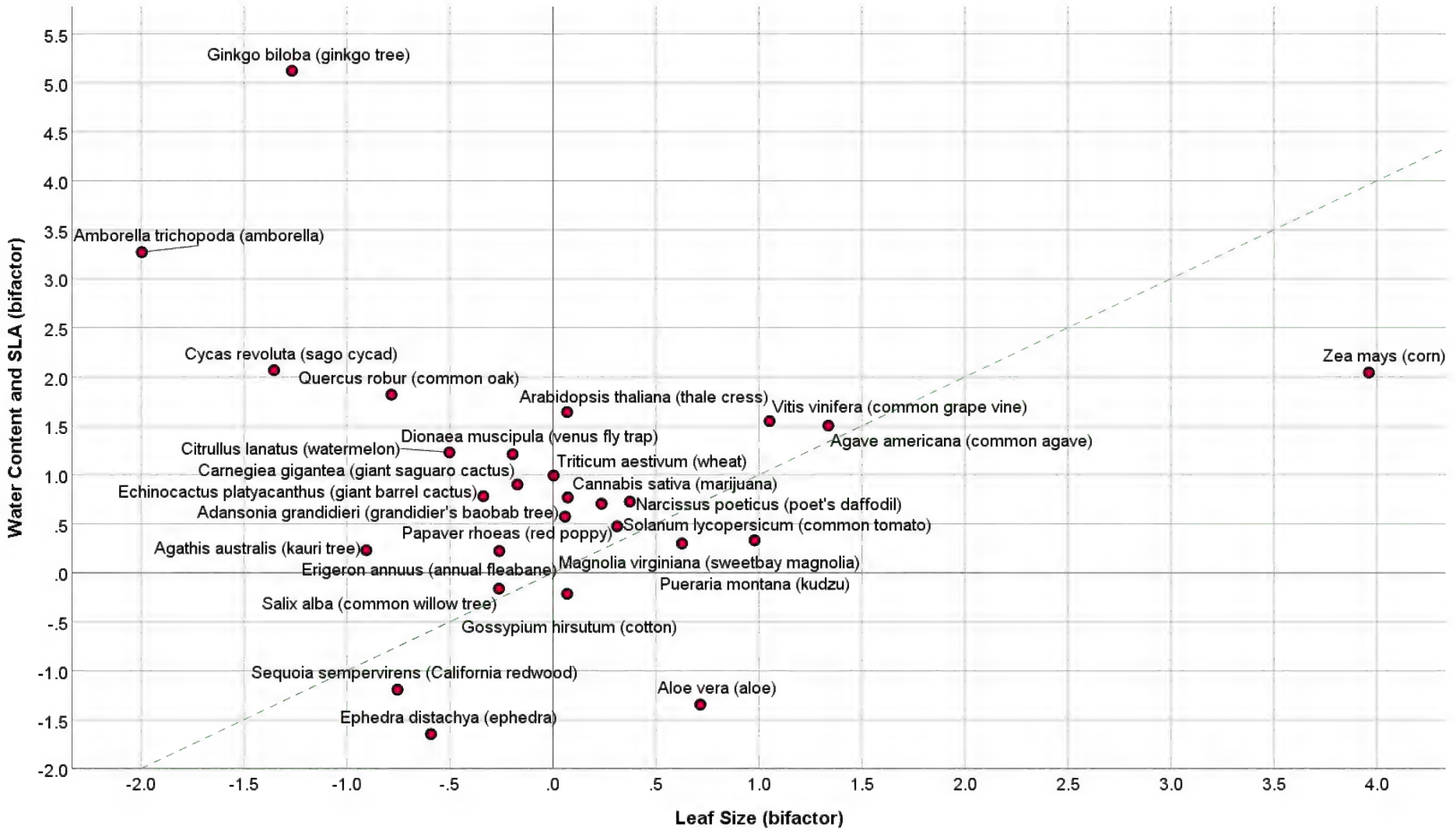

Figure 8. Selected species examples showing relative standing on Leaf Size and SLA/Water Content scores produced from a bifactor model. Scores are independent (uncorrelated); any visual hint of a relationship between scores is due only to this specific set of examples; the purpose of the plot is only to show where some common plants score relative to one another, not to show a bivariate relationship; dotted line is identity line (x = y)**, not line of best fit**.

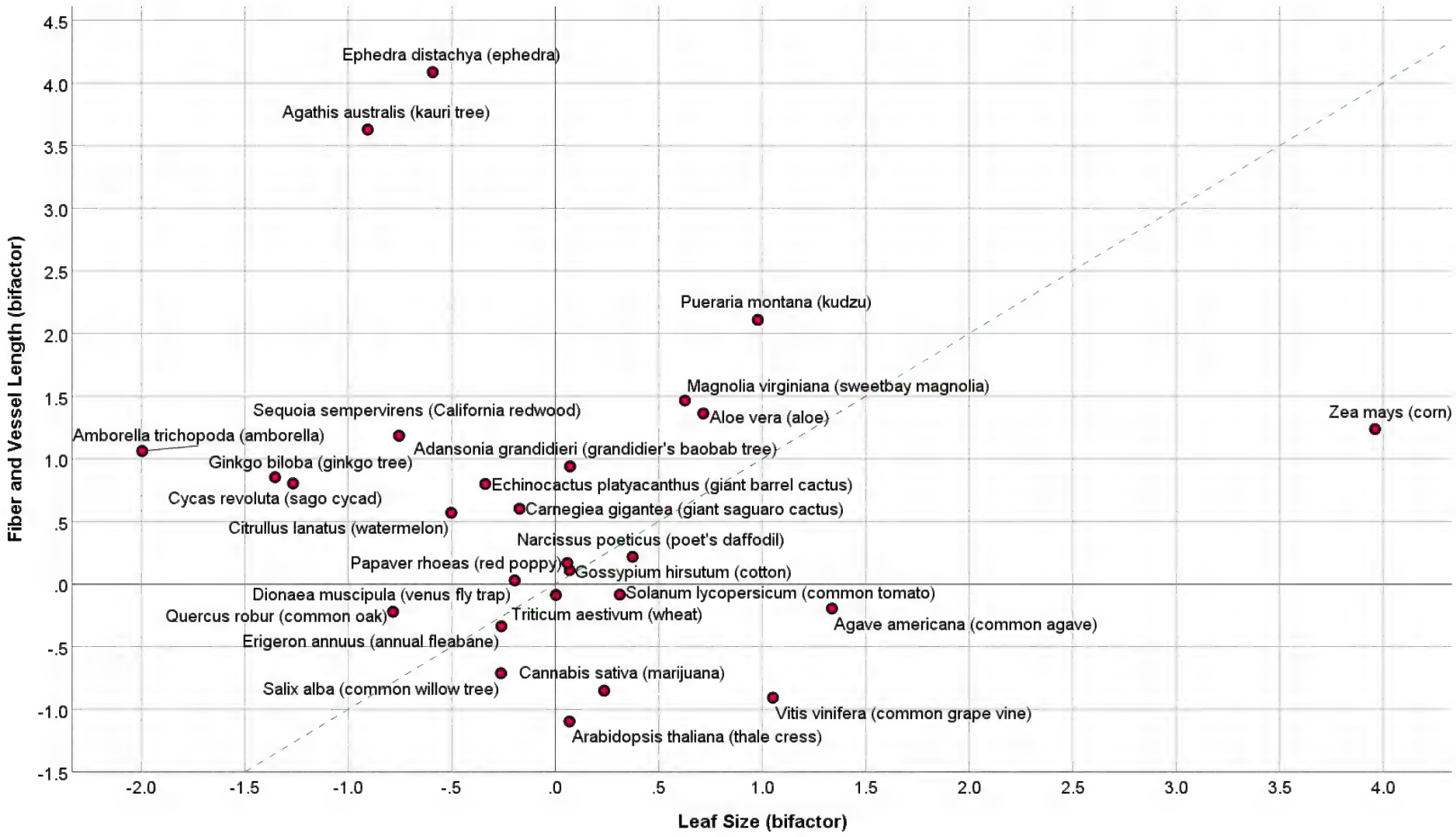

Figure 9. Selected species examples showing relative standing on Leaf Size and Fiber/Vessel Length scores produced from a bifactor model. Scores are independent (uncorrelated); any visual hint of a relationship between scores is due only to this specific set of examples; the purpose of the plot is only to show where some common plants score relative to one another, not to show a bivariate relationship; dotted line is identity line (x = y)**, not line of best fit**.

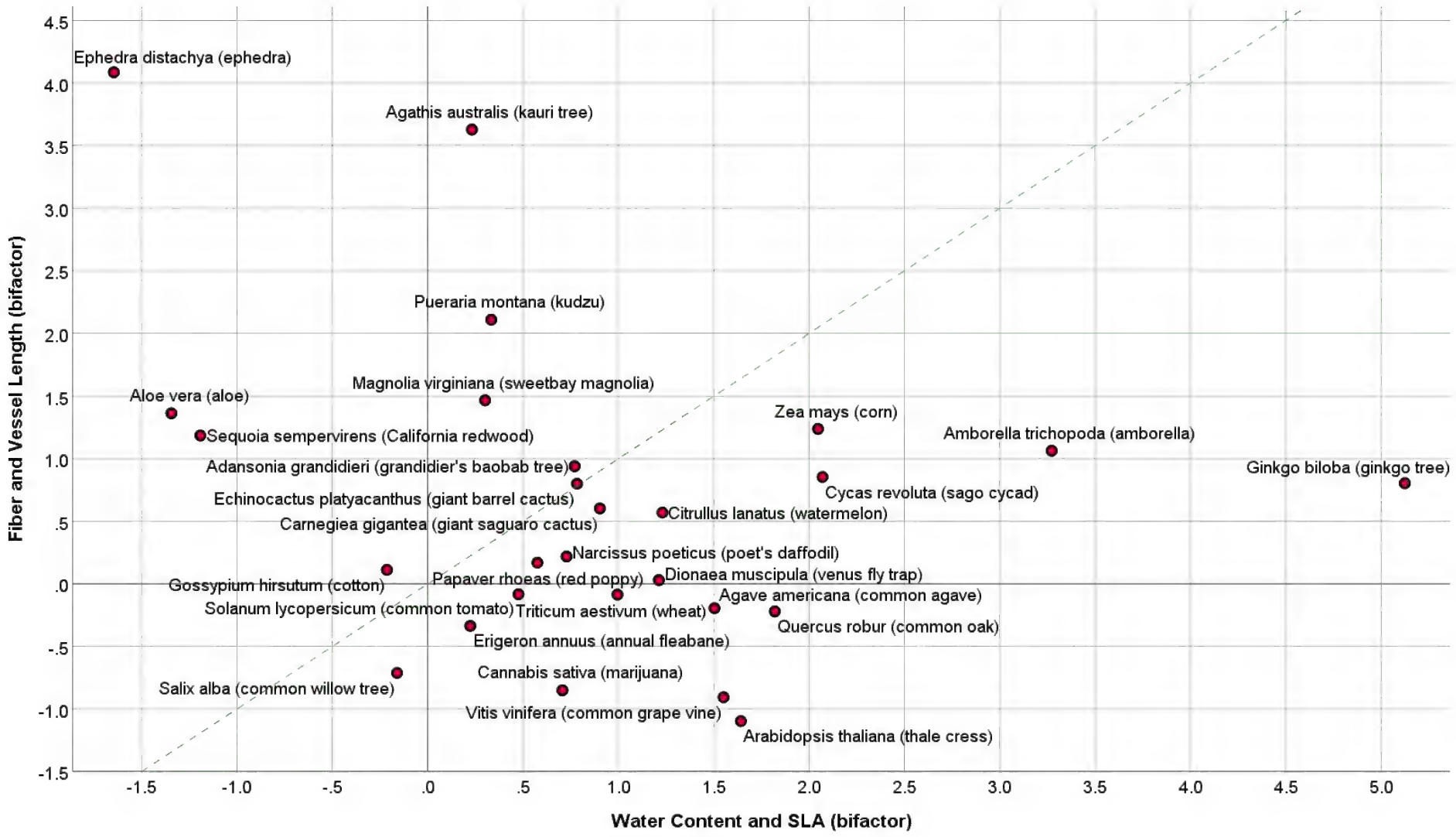

Figure 10. Selected species examples showing relative standing on SLA/Water Content and Vessel/Fiber Length scores produced from a bifactor model. Note: scores are independent (uncorrelated); any visual hint of a relationship between scores is due only to this specific set of examples; the purpose of the plot is only to show where some common plants score relative to one another, not to show a bivariate relationship; dotted line is identity line (x = y)**, not line of best fit**.

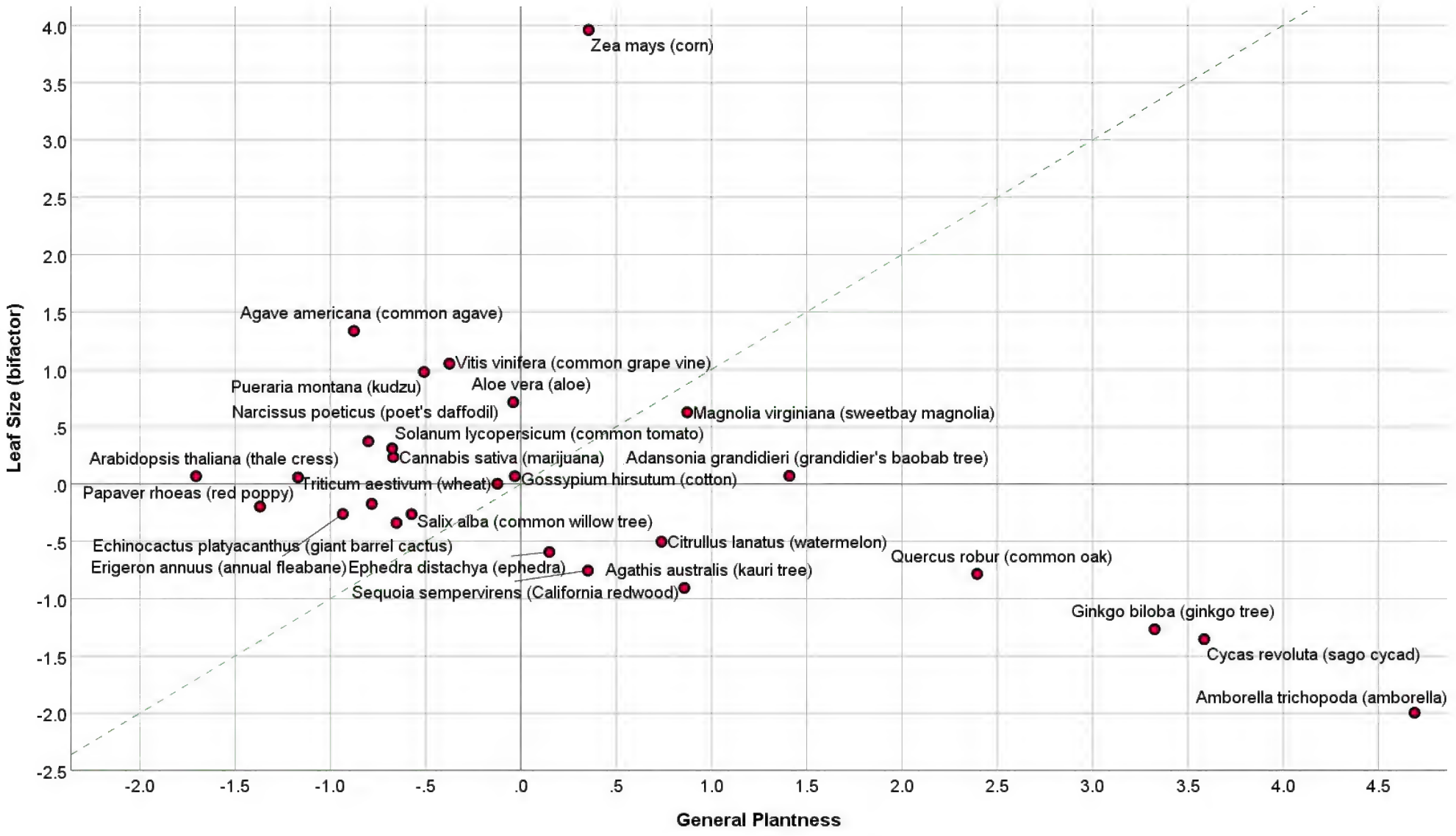

Figure 11. Selected plant examples showing relative standing on General Plantness and Leaf Size scores produced from a bifactor model. Note: scores are independent (uncorrelated); any visual hint of a relationship between scores is due only to this specific set of examples; the purpose of the plot is only to show where some common plants score relative to one another, not to show a bivariate relationship; dotted line is identity line (x = y)**, not line of best fit**.

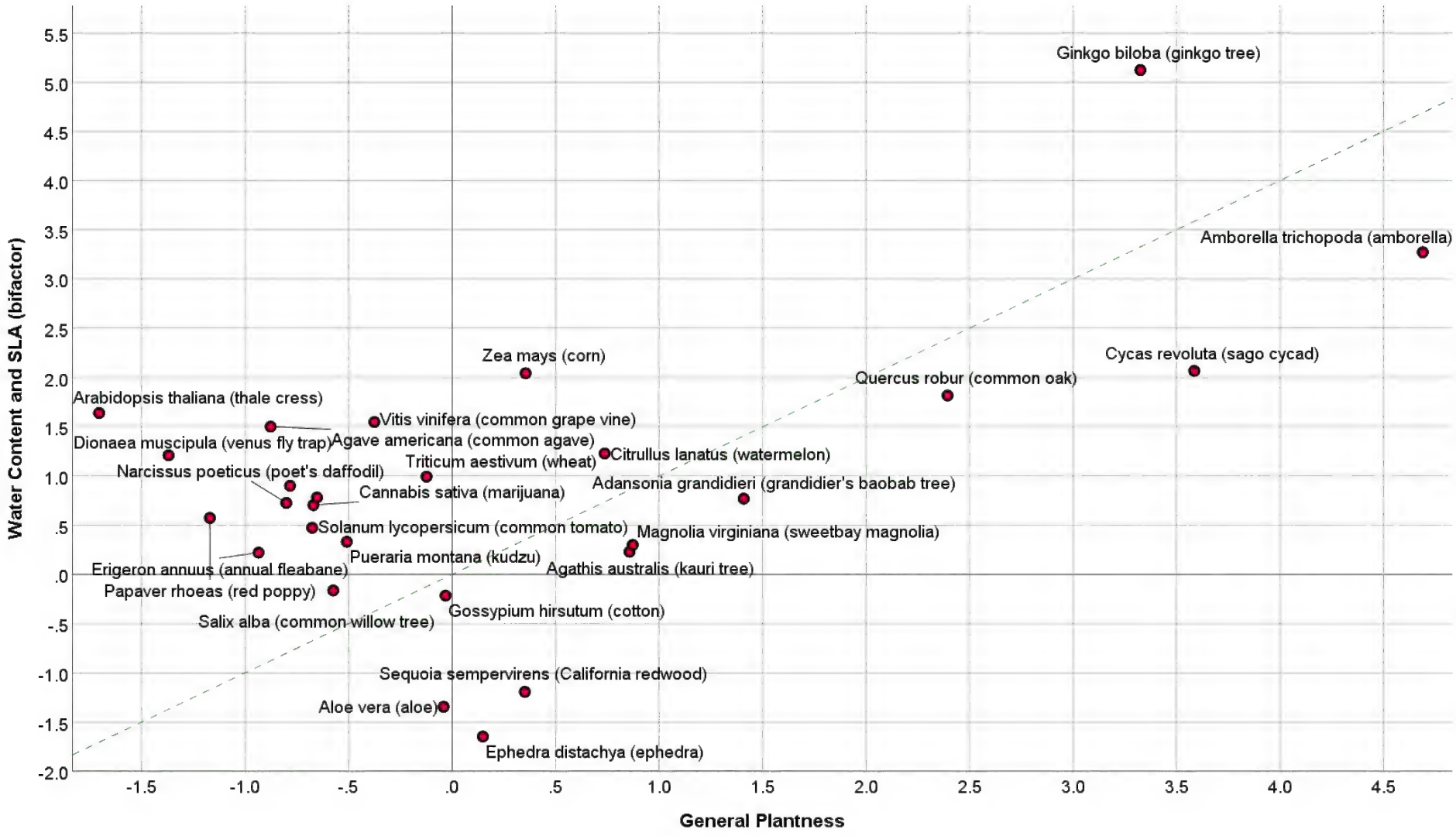

Figure 12. Selected plant examples showing relative standing on General Plantness and SLA Water Content scores produced from a bifactor model. Note: scores are independent (uncorrelated); any visual hint of a relationship between scores is due only to this specific set of examples; the purpose of the plot is only to show where some common plants score relative to one another, not to show a bivariate relationship; dotted line is identity line (x = y)**, not line of best fit**.

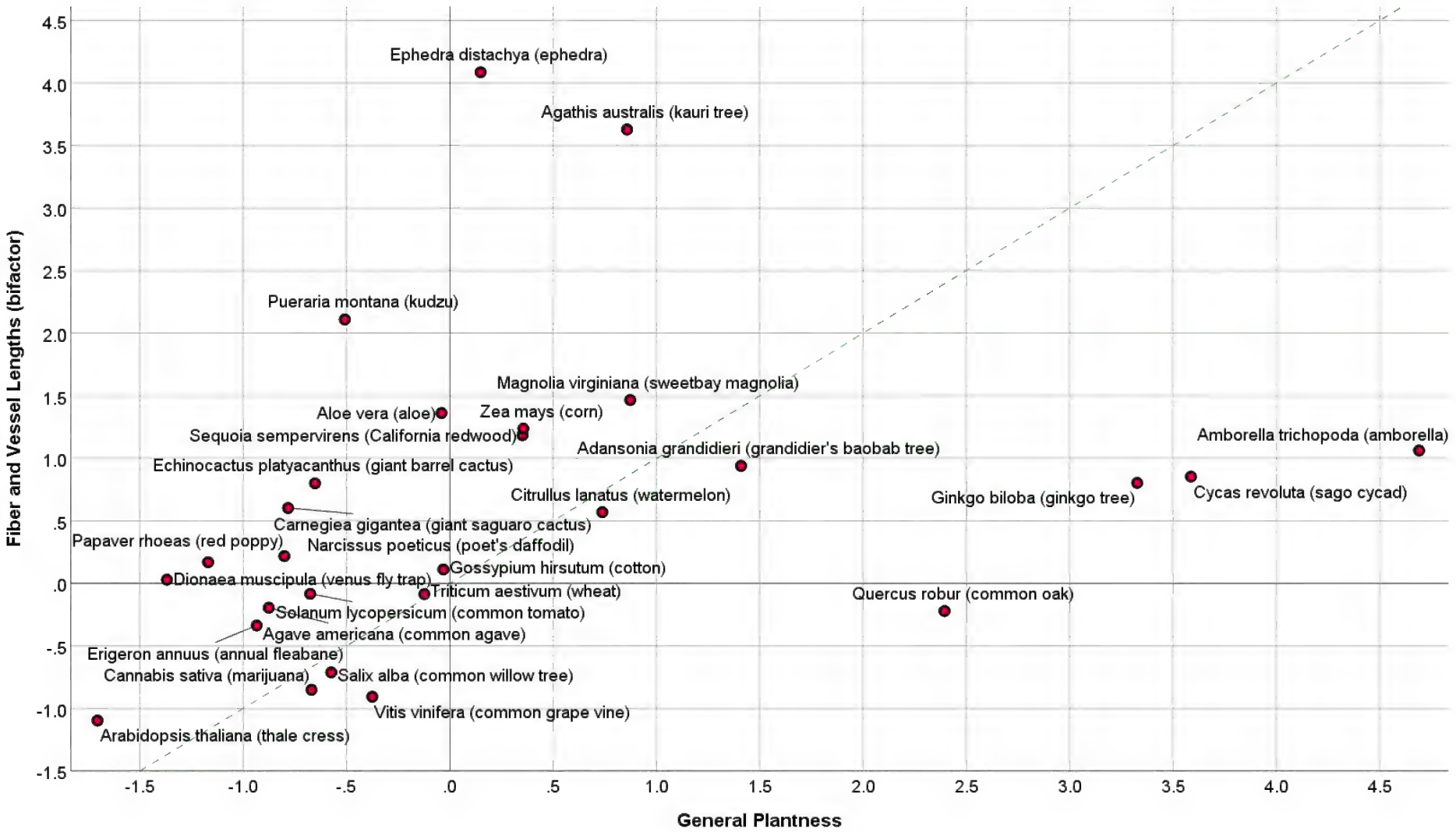

Figure 13. Selected plant examples showing relative standing on General Plantness and Fiber/Vessel Length scores produced from a bifactor model. Note: scores are independent (uncorrelated); any visual hint of a relationship between scores is due only to this specific set of examples; the purpose of the plot is only to show where some common plants score relative to one another, not to show a bivariate relationship; dotted line is identity line (x = y)**, not line of best fit**.

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TYPIFICATION OF *HETEROTHECA VILLOSA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

An earlier selection for neotype of *Amellus villosus* Pursh is interpreted as a plant of *Heterotheca ballardii* and is superseded by a different choice. Both the earlier and current choice are Nuttall collections from along the Missouri River in 1811 and are mounted on the same PH sheet.

Authentic type material for *Amellus villosus* Pursh (1814) cannot be located (Semple 1990, confirmed here). It is argued here that Semple (1990) inadvertently chose as neotype of *A. villosus* a specimen more closely matching the type of *Chrysopsis ballardii* Rydb. than the taxon to which the names *A. villosus* and *Heterotheca villosa* (Pursh) Shinners sensu stricto have been applied. If Semple's choice is followed, the name *H. villosa* (Pursh) Shinners sensu stricto must be applied to plants that have been identified as *H. villosa* var. *ballardii* (Rydb.) Semple and a different name must be applied to plants traditionally identified as *H. villosa* (*Chrysopsis foliosa* Nutt. 1841 and *Chrysopsis mollis* Nutt. 1841 are available). The course taken here is to supersede Semple's choice of neotype, maintaining the traditional concepts and nomenclature for "ballardii" and "villosa."

In the protologue for *Amellus villosus*, Pursh (1814) cited plants collected by John Bradbury, who was a member of the Astorian expedition (Bradbury 1817; Wikipedia 2016; World Heritage Encyclopedia 2016). Thomas Nuttall also was a member of the expedition and made collections. Bradbury's collections were quickly sent to England, where Pursh studied them.

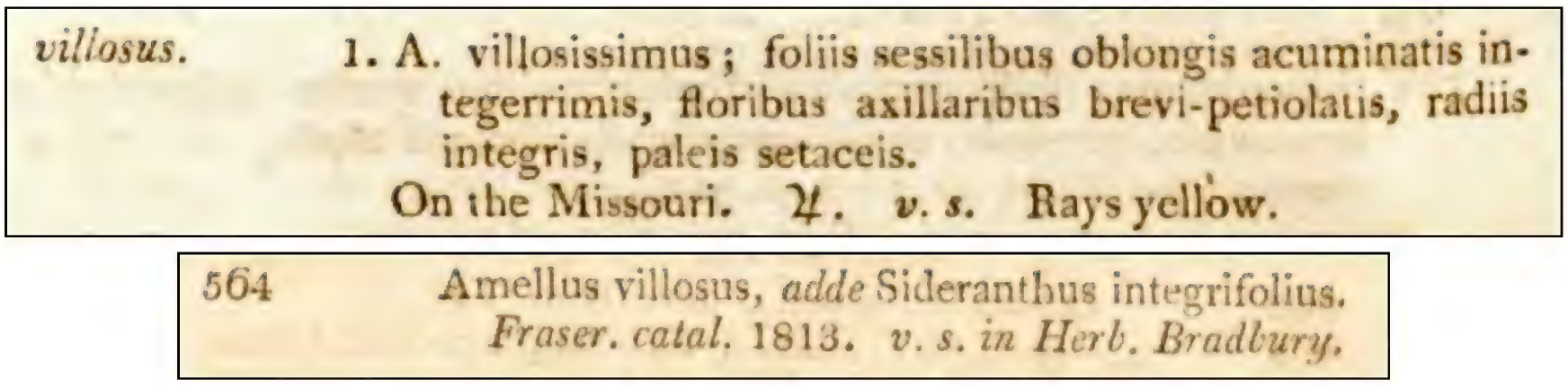
The Astorian expedition set out from St. Louis, Missouri, in mid March 1811 and traveled up the Missouri River, on 12 June reaching a cluster of Arikara Indian villages near the confluence of the Grand and Missouri rivers, near present-day Mobridge in Walworth County, South Dakota (Fig. 1). From there a party including Bradbury and Nuttall traveled farther upriver, on 20 June reaching Fort Lisa (referred to by Bradbury as "Fort Mandan") in present North Dakota, just north of what is now Stanton in Mercer County. From there, they returned downstream, leaving 26 June, to the Arikara site, where they remained until both Bradbury and Nuttall departed on 17 August and returned directly to St. Louis.

Figure 1. Sites of the Arikara Indian villages (blue, South Dakota) and Fort Lisa (red, North Dakota) along the Missouri River (blue highlight). John Bradbury and Thomas Nuttall were at and between these sites in 1811 and the type collection of *Amellus villosus* probably was made somewhere along this ca. 160 mile stretch. Plants identified as "villosa" and "ballardii" are sympatric in this area (see Maps 3 and 5 in Nesom 2020).

As related by Semple (1990), Pursh drew the description of *Amellus villosus* from a Bradbury collection that he saw either at LIV in Liverpool or in the Lambert Herbarium (at Lambert's estate in Boyton, England). In the protologue, Pursh indicated "v.s." in the main text (p. 564) and "v.s. in Herb. Bradbury" in the Supplementum, (p. 750; see Figs. 2 and 3). In the preface to his flora (p. xvii), Pursh noted that "I am also highly indebted to William Roscoe, Esq. [at the Liverpool Botanic Garden], who very obligingly communicated to me Mr. Bradbury's Plants collected in Upper Louisiana."

One Bradbury collection of *Heterotheca* is extant in the LIV herbarium, identified by Semple as *H. camporum* (Greene) Shinners. It is without locality data. *Heterotheca camporum* occurs in the vicinity of the Missouri River in east-central Missouri (near St. Louis) and Bradbury probably made the collection there in 1810 before setting out with the Astorian expedition. The Astorian expedition as it moved upriver was quickly out of the geographic range of *H. camporum* and too early in its flowering season. Vestiture of *H. camporum* would not be characterized as "villosissimus," and, as noted by Semple, the leaves of *H. camporum* characteristically are serrate (contrasting with the Pursh protologue for "villosus").

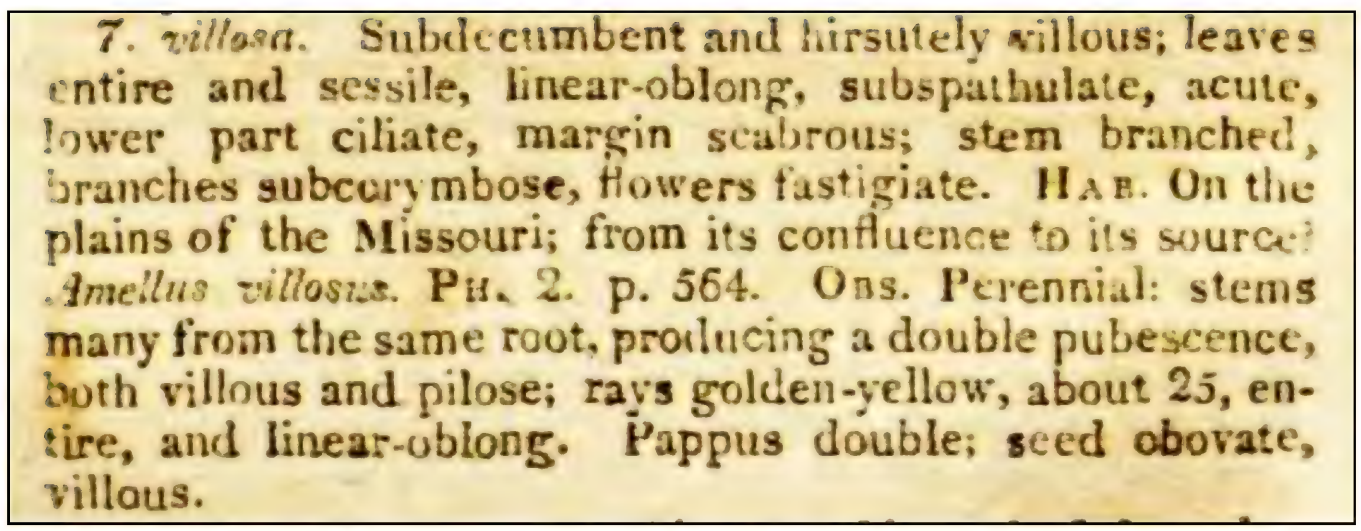
Pursh's diagnosis for *Amellus villosus* (Fig. 2) could match numerous species of *Heterotheca*; his specification of "on the Missouri" as the type locality and the timing of his publication (in late 1813, closely following the Astorian expedition) make it probable that the plant was either 'villosa' or 'ballardii,' the only two heterothecas (other than *H. angustifolia* in southern South Dakota and *H. camporum*) that occur on the expedition's route along the Missouri River. Pursh's phrase "floribus axillaribus brevi-petiolatis" seems to match Nuttall's more specific description in 1818 of *Inula villosa* (Fig. 3) as "branches subcorymbose, flowers fastigiate," in which case both descriptions probably referred to *H. villosa* as currently understood. Nuttall's description could not apply to "ballardii" (see comments below).



villosus. 1. A. villosissimus; foliis sessilibus oblongis acuminatis integerrimis, floribus axillaribus brevi-petiolatis, radiis integris, paleis setaceis.
On the Missouri. ♃. *v. s.* Rays yellow.

564 Amellus villosus, *adde* Sideranthus integrifolius.
Fraser. catal. 1813. *v. s. in Herb. Bradbury.*

Figure 2. Pursh's 1814 main entry for *Amellus villosus*, p. 564 (above, main entry) and p. 750 (below, Supplementum, referring to p. 564).



7. villosa. Subdecumbent and hirsutely villous; leaves entire and sessile, linear-oblong, subspathulate, acute, lower part ciliate, margin scabrous; stem branched, branches subcorymbose, flowers fastigiate. HAB. On the plains of the Missouri; from its confluence to its source? *Amellus villosus.* PH. 2. p. 564. OBS. Perennial: stems many from the same root, producing a double pubescence, both villous and pilose; rays golden-yellow, about 25, entire, and linear-oblong. Pappus double; seed obovate, villous.

Figure 3. Nuttall's 1818 description of *Inula villosa* (Pursh) Nutt. The phrases "branches subcorymbose, flowers fastigiate" and "stems ... producing a double pubescence, both villous and pilose" refer to *Heterotheca villosa* as traditionally understood, not to *Heterotheca ballardii*.

Semple choice of neotype for *Amellus villosus* is a Nuttall collection at PH with Nuttall's handwritten annotation as "Chrysopsis *villosa, Missouri." The PH sheet has 3 stems, all three identified by the single Nuttall label — Semple's annotation notes that "The three *Nuttall s.n.* collections are from different plants" (as also observed earlier by Lloyd Shinners by annotation of the PH sheets; I agree). Stem 1 (Semple's neotype) in the concept here is "ballardii." Stem 2 is "villosa." Stem 3 is "camporum."

Figure 4. Sheet at PH with three *Nuttall* collections (all originally as "001726") from along the Missouri River. Stem 1 is Semple's neotype of *Amellus villosus*, identified here as "ballardii;" stem 2 is my choice of neotype for *A. villosus*; stem 3 is conspecific with the lectotype of *Heterotheca camporum* (Greene) Shinners.

Semple (1990, p. 224) wrote that "Nuttall may have penned the name "Chrysopsis *villosa" on his collection in the field in 1811. If Bradbury was aware of this (they did travel together) and added it to a label of his collection of the same taxon along with location data, then Pursh may have seen the epithet and adopted it." Semple's interpretation seems likely to me, with the caveat that stems 1 and 2 probably were recognized by Nuttall in the field as different in growth habit and vestiture.

Stem 1 (PH 24816, Semple's neotype). This stem has relatively long peduncles with solitary heads without capitular bracts, like "ballardii," but the vestiture is antrorsely loosely strigose-villous, more like "villosa." The stem vestiture of "villosa" in the Dakotas region is characteristically 2-storied; that of stem 1 is single-storied. I identify stem 1 as "ballardii" perhaps with influence (in vesiture) of "villosa." The type of *Chrysopsis ballardii* (Fig. 7) has vestiture similar to stem 1, PH 24816, not like that more characteristic of "ballardii" over its range, and it perhaps also is introgressed from *H. villosa*. Semple (1990, p. 224) noted that "Shinners apparently rejected [stem 1] as a match for Nuttall's taxon for lack of a double pubescence, but the fragment does have this trait as well as 'flowers fastigiate' and an apparently more subdecumbent habit." I do not see a "fastigiate" arrangement of heads or the "double pubescence" on stem 1.

Stem 2 (PH 2717, designated here as neotype, superseding the previous choice). The stem vestiture is 2-storied, matching "villosa." The single head appears to be solitary on a stem densely leaf to immediately below the head (see Fig. 4 inset); this evidently is an early-season stem with distal axillary buds that would have formed a closely corymboid ('fastigate') capitulescence characteristic of "villosa" (see comparable stem and expanded inset in Fig. 5; characteristic morphology in Fig. 6). The resemblance in vestiture between PH 2717 and traditionally identified "villosa" also was noticed by L.H. Shinners; his handwritten note in annotation, pointing to stem 2, says that "This is the only one of these three obviously unrelated fragments having the double pubescence described by Nuttall, but it does not appear to be subdecurrent with corymbose, fastigiate inflorescence."

Amellus villosus Pursh, Fl. Amer. Sept. 2: 564 and 750. 1814 [1813]. *Inula villosa* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 151. 1818. *Diplopappus villosus* (Pursh) Hook., Fl. Bor.-Amer. 2: 22. 1834. *Chrysopsis villosa* (Pursh) Nutt. ex DC., Prodr. 5: 327. 1836. *Diplogon villosum* (Pursh) Kuntze , Revis. Gen. Pl. 1: 334. 1891. *Heterotheca villosa* (Pursh) Shinners, Field & Lab. 19: 71. 1951. **TYPE**: **USA**. [**South Dakota** or **North Dakota**]. Protologue: "On the Missouri," June or early July, *J. Bradbury s.n.* (holotype: apparently lost or destroyed, fide Semple 1990).

Superceded NEOTYPE (Semple 1990, p. 225): ["UNITED STATES. Missouri, [in 1811], *Nuttall s.n.* (PH-001726!, shoot no. 1)," Fig. 4. Locality as deduced: Along the Missouri River in South Dakota or North Dakota, July or August, 1811. The left stem (shoot no. 1) of the original three stems of "PH-1726" has a barcode of 00024816.

New NEOTYPE (designated here): Label: "Missouri, Nuttall." Locality as deduced: Along the Missouri River in South Dakota or North Dakota, July or August 1811, *T. Nuttall s.n.* (PH-001726/00002717!, stem no. 2, and digital image!, Fig. 4).

Figure 5. *Heterotheca villosa* sensu stricto (in sense of the present study; *H. villosa* var. *villosa* as annotated by Semple 1993). *Larson 5370* (MIN) from Dunn Co., North Dakota. Early season collection. Inset shows first head on immature branch, with axillary buds below; typical corymboid arrangement of heads developing on 2 branches on right. This morphology is similar to that of the new designated neotype (Fig. 4, stem 2).

Figure 6. *Heterotheca villosa*, characteristic morphology of closely corymboid capitulescence (heads "fastigiate"), heads with capitular bracts, and 2-storied stem vestiture. *Roberts s.n.* (MIN) from Hennepin Co., Minnesota.

Figure 7. Holotype of *Chrysopsis ballardii* (MIN), from Chaska in Carver Co., Minnesota.

Figure 8. Representative specimen of "ballardii" (in sense of the present study; *H. villosa* var. *ballardii* as annotated by Semple 1993). *Stephens 12607* (MIN) from Mercer Co., North Dakota.

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I'm grateful to John Strother for his helpful review and editing and staff at PH for their hospitality.

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TAXONOMIC SUMMARY OF *HETEROTHECA* (ASTERACEAE: ASTEREAE): SECT. *CHRYSANTHE*

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ABSTRACT

A taxonomic overview of *Heterotheca* sect *Chrysanthe* includes 49 species. Fourteen new species are described: **Heterotheca excelsior** Nesom, **sp. nov.**, **Heterotheca fulciens** Nesom, **sp. nov.**, **Heterotheca hartmanii** Nesom, **sp. nov.**, **Heterotheca incensa** Nesom, **sp. nov.**, **Heterotheca inflata** Nesom, **sp. nov.**, **Heterotheca joshuana** Nesom, **sp. nov.**, **Heterotheca komarekiae** Nesom, **sp. nov.**, **Heterotheca marcbakeri** Nesom, **sp. nov.**, **Heterotheca orovillosa** Nesom, **sp. nov.**, **Heterotheca postpetrinis** Nesom, **sp. nov.**, **Heterotheca scelionis** Nesom, **sp. nov.**, **Heterotheca schneideri** Nesom, **sp. nov.**, **Heterotheca utahensis** Nesom, **sp. nov.**, and **Heterotheca vespertina** Nesom, **sp. nov.** Two new combinations validate earlier names for currently recognized species: **Heterotheca hirsuta** (Greene) Nesom, **comb. nov.** (replacing *H. barbata* and modifying its definition) and **Heterotheca hirsutissima** (Greene) Nesom, **comb. nov.** (replacing *H. horrida*). One replacement name is required: **Heterotheca paniculata** Nesom, **nom. nov.** (= *Chrysopsis floribunda* Greene, not *Heterotheca floribunda* Benth.). Nine new combinations validate names at specific rank in *Heterotheca*, drawn from species previously described in *Chrysopsis* and from taxa previously treated at varietal rank within *Heterotheca*: **Heterotheca angustifolia** (Rydb.) Nesom, **comb. nov.**, **Heterotheca ballardii** (Rydb.) Nesom, **comb. nov.**, **Heterotheca cinerascens** (Blake) Nesom, **comb. et stat. nov.**, **Heterotheca cryptocephala** (Woot. & Standl.) Nesom, **comb. nov.**, **Heterotheca harmsiana** (Semple) Nesom, **comb. et stat. nov.**, **Heterotheca hispida** (Hook.) Nesom, **comb. nov.**, **Heterotheca pedunculata** (Greene) Nesom, **comb. nov.**, **Heterotheca resinolens** (A. Nels.) Nesom, **comb. nov.**, and **Heterotheca scabrifolia** (A. Nels.) Nesom, **comb. nov.** A lectotype is designated for *Chrysopsis floribunda* Greene. Details of typification, a county-level distribution map, and at least a diagnostic description are provided for each species.

This study follows the treatment of sects. *Heterotheca* and *Ammodia* (Nesom, Phytoneuron 2019-64: 1–22. 2019), which gives an introduction, Acknowledgements, and Literature Cited for the whole series. A treatment of sect. *Phyllotheca* is in preparation.

Hopes of resolving several taxonomic problems in goldenasters by field and herbarium study in 2020 were nixed by the pandemic — the study is published in its present form to substantiate usage of names in floristic accounts. Modifications and additions probably will be made in the near future.

INDEX and MAPS — HETEROTHECA sect. CHRYSANTHE

		MAPS
[part 1: 1–74]		
1. H. polothrix Nesom	p. 19	Map 1/ Fig. 1
2. H. excelsior Nesom	p. 24	Map 1/ Figs. 1, 4
3. H. cinerascens (Blake) Nesom	p. 32	Map 1/ Fig. 1
4. H. joshuana Nesom	p. 39	Map 1/ Fig. 1
5. H. shevockii Semple	p. 42	Map 1/ Fig. 1
6. H. hirsuta (Greene) Nesom	p. 42	Map 2/ Fig. 11
7. H. scelionis Nesom	p. 55	Map 2/ Figs. 16, 23
8. H. vespertina Nesom	p. 62	Map 3/ Fig. 29
9. H. orovillosa Nesom	p. 67	Map 4/ Fig. 33

[part 2: 75–134]

10. H. hispida (Hook.) Nesom	p. 77	Map 5/ Fig. 38
11. H. villosa (Pursh) Shinners	p. 82	Map 3/ Figs. 29, 38
12. H. ballardii (Rydb.) Nesom	p. 86	Map 5/ Fig. 38
13. H. canescens (DC.) Shinners	p. 88	Map 6/ Fig. 46
14. H. angustifolia (Rydb.) Nesom	p. 96	Map 7/ Fig. 53
15. H. stenophylla (A. Gray) Shinners	p. 103	Map 8/ Fig. 59
16. H. scabrifolia (A. Nels.) Nesom	p. 104	Map 8/ Fig. 59
17. H. wisconsinensis (Shinners) Shinners	p. 126	Map 5/ Fig. 38
18. H. camporum (Greene) Shinners	p. 129	Map 9/ Fig. 83
19. H. brandegeei (Rob. & Greenm.) Semple	p. 134	Map 1/ Fig. 1
20. H. jonesii (Blake) Welsh & Atwood	p. 134	Map 11/ Fig. 106

[part 3: 135–216]

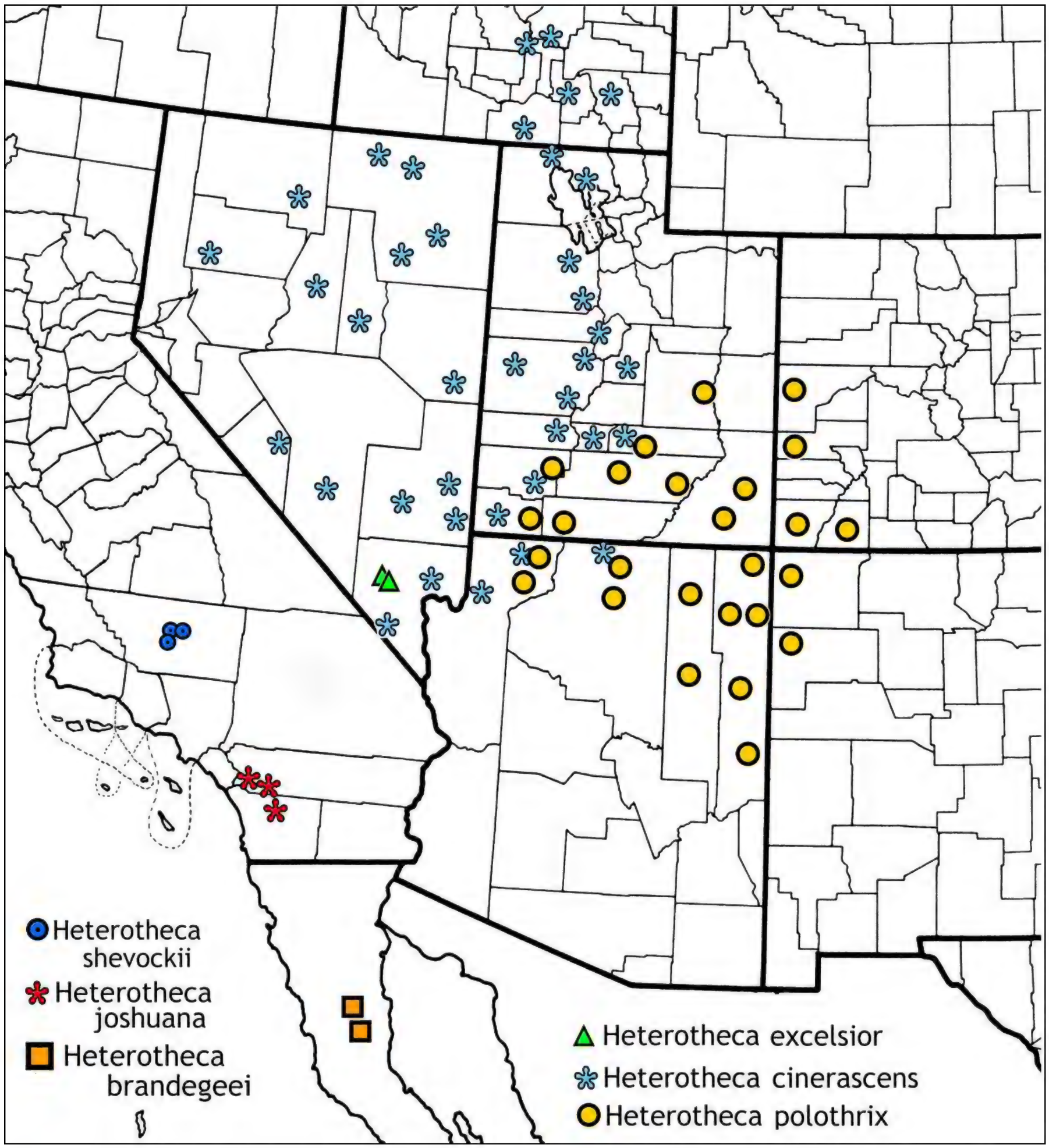
21. H. loboensis Nesom	p. 135	Map 10/ Figs. 84, 91
22. H. zionensis Semple	p. 144	Map 10/ Fig. 91
23. H. utahensis Nesom	p. 155	Map 10/ Fig. 91
24. H. pedunculata (Greene) Nesom	p. 160	Map 11/ Fig. 106
25. H. inflata Nesom	p. 181	Map 13/ Fig. 108
26. H. depressa (Rydb.) Dorn	p. 191	Map 11/ Figs. 106, 131
27. H. incensa Nesom	p. 201	Map 12/ Fig. 107

[part 4: 217–319]

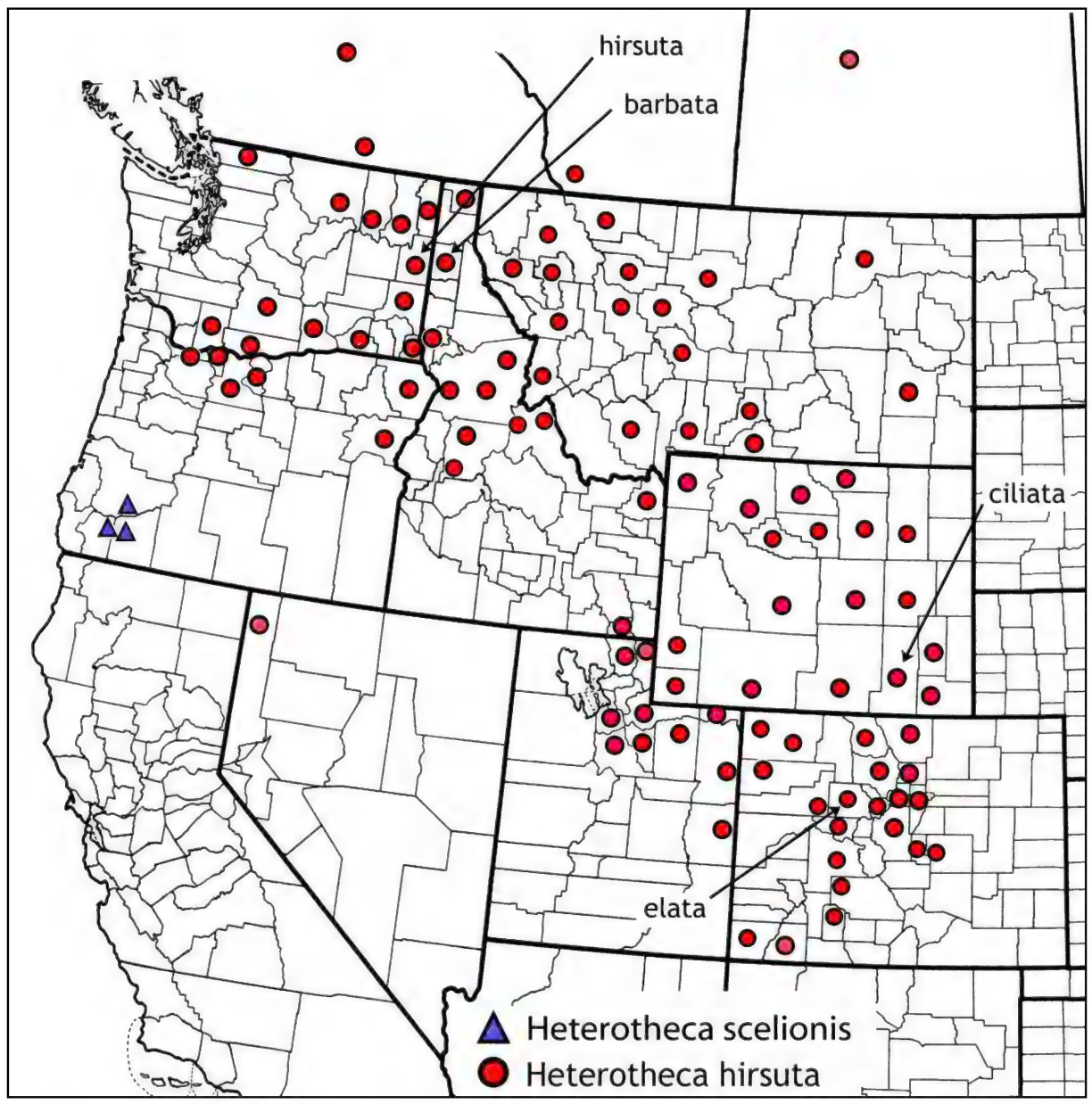
28. H. postpetrinis Nesom	p. 217	Map 16/ Figs. 134, 210
29. H. hartmanii Nesom	p. 222	Map 11/ Fig. 98
30. H. hirsutissima (Greene) Nesom	p. 229	Map 13/ Fig. 141
31. H. sierrablancensis (Semple) Nesom	p. 242	Map 13/ Fig. 141
32. H. rutteri (Rothr.) Shinners	p. 248	Map 14/ Fig. 155
33. H. mucronata Harms ex Turner	p. 250	Map 18/ Fig. 156
34. H. gypsophila Turner	p. 250	Map 18/ Fig. 156
35. H. harmsiana (Semple) Nesom	p. 250	Map 18/ Fig. 156
36. H. mexicana Harms ex Turner	p. 257	Map 18/ Fig. 156
37. H. viscida (A. Gray) Harms	p. 258	Map 14/ Fig. 155
38. H. komarekiae Nesom	p. 263	Map 16/ Figs. 167, 210
39. H. resinolens (A. Nels.) Nesom	p. 268	Map 17/ Fig. 235
40. H. paniculata Nesom	p. 271	Map 17/ Fig. 235
41. H. pumila (Greene) Semple	p. 292	Map 16/ Fig. 210
42. H. schneideri Nesom	p. 306	Map 16/ Fig. 210

[part 5: 320–359]

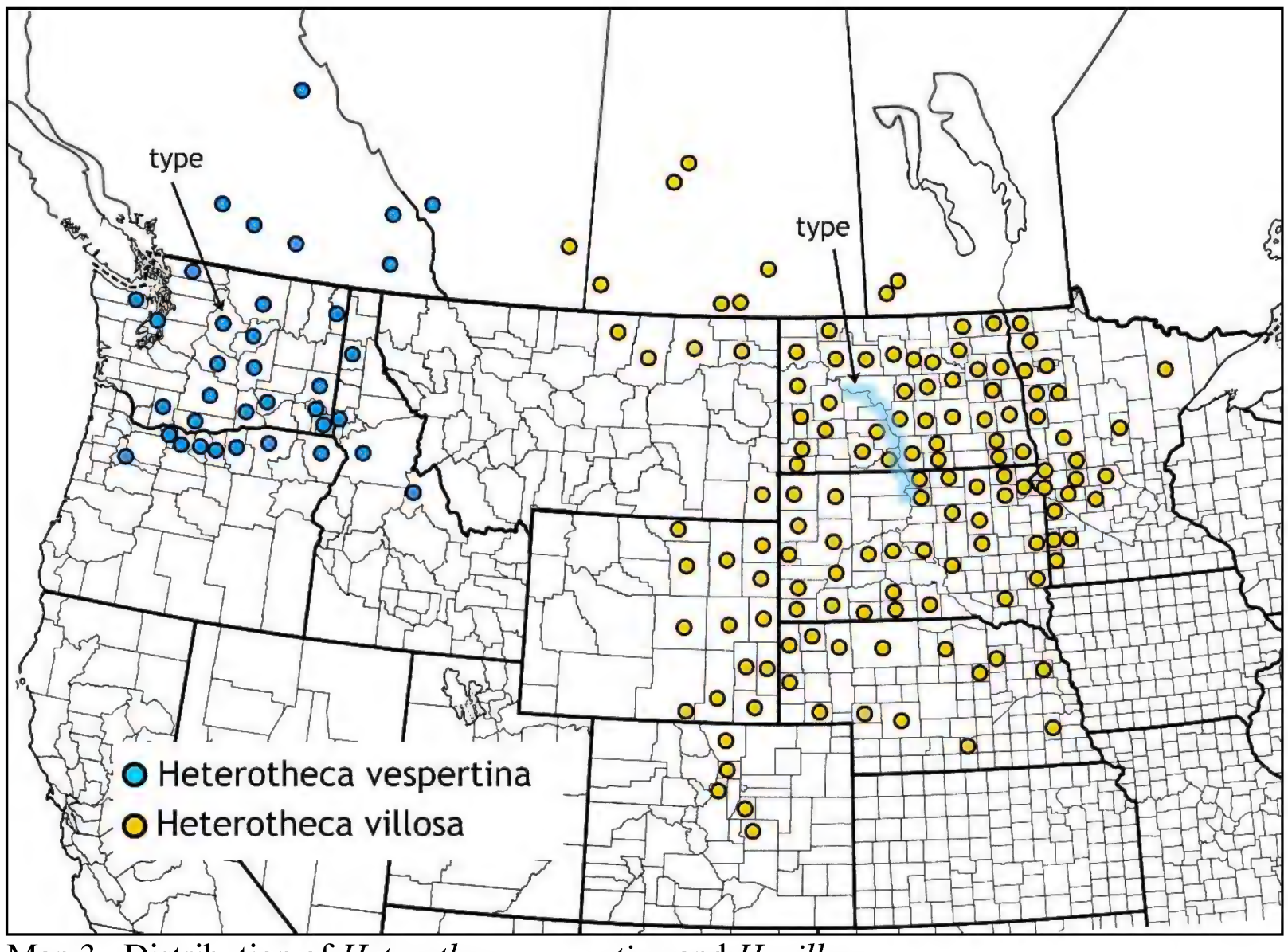
43. H. fulciens Nesom	p. 320	Map 17/ Fig. 235
44. H. marcbakeri Nesom	p. 329	Map 17/ Figs. 235, 245
45. H. marginata Semple	p. 335	Map 14/ Fig. 155
46. H. arizonica (Semple) Nesom	p. 339	Map 15/ Fig. 248
47. H. fulcrata (Greene) Shinners	p. 345	Map 17/ Fig. 235
48. H. cryptocephala (Woot. & Standl.) Nesom	p. 351	Map 17/ Fig. 235
49. H. nitidula (Woot. & Standl.) Nesom	p. 354	Map 17/ Fig. 235



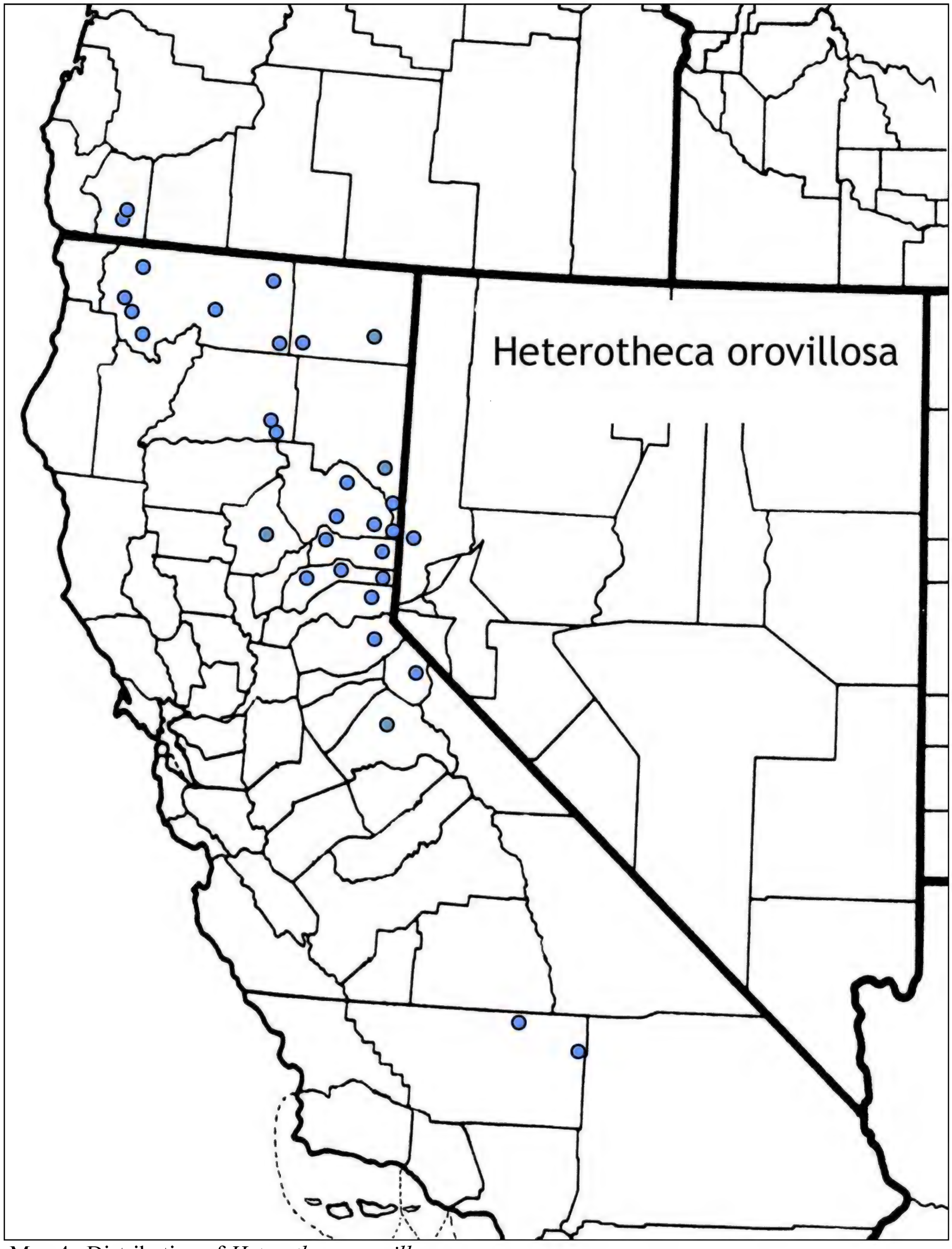
Map 1. Distribution of *Heterotheca* species.



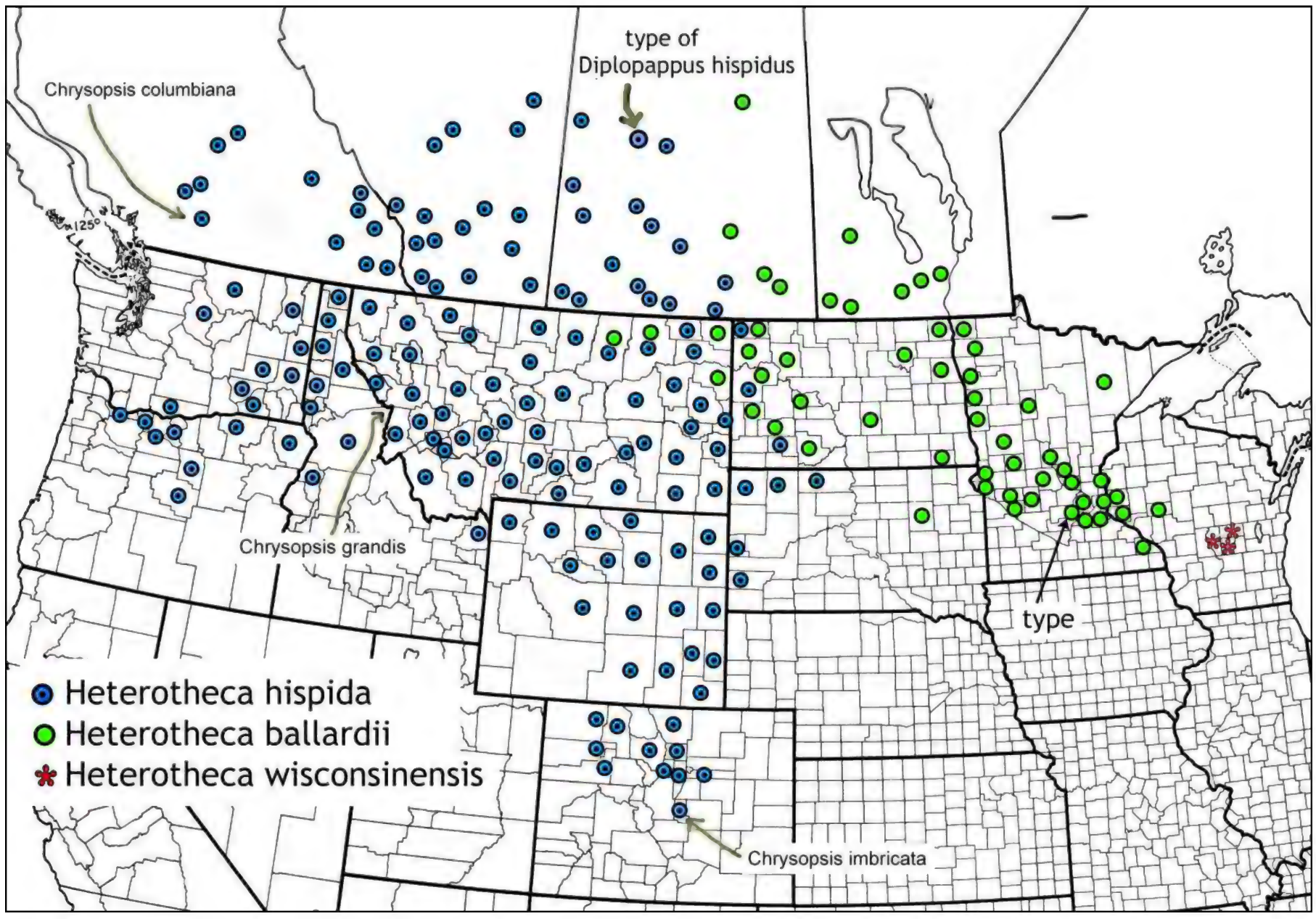
Map 2. Distribution of *Heterotheca scelionis* and H. *hirsuta*. Names with arrows are for synonyms of *H. hirsuta*.



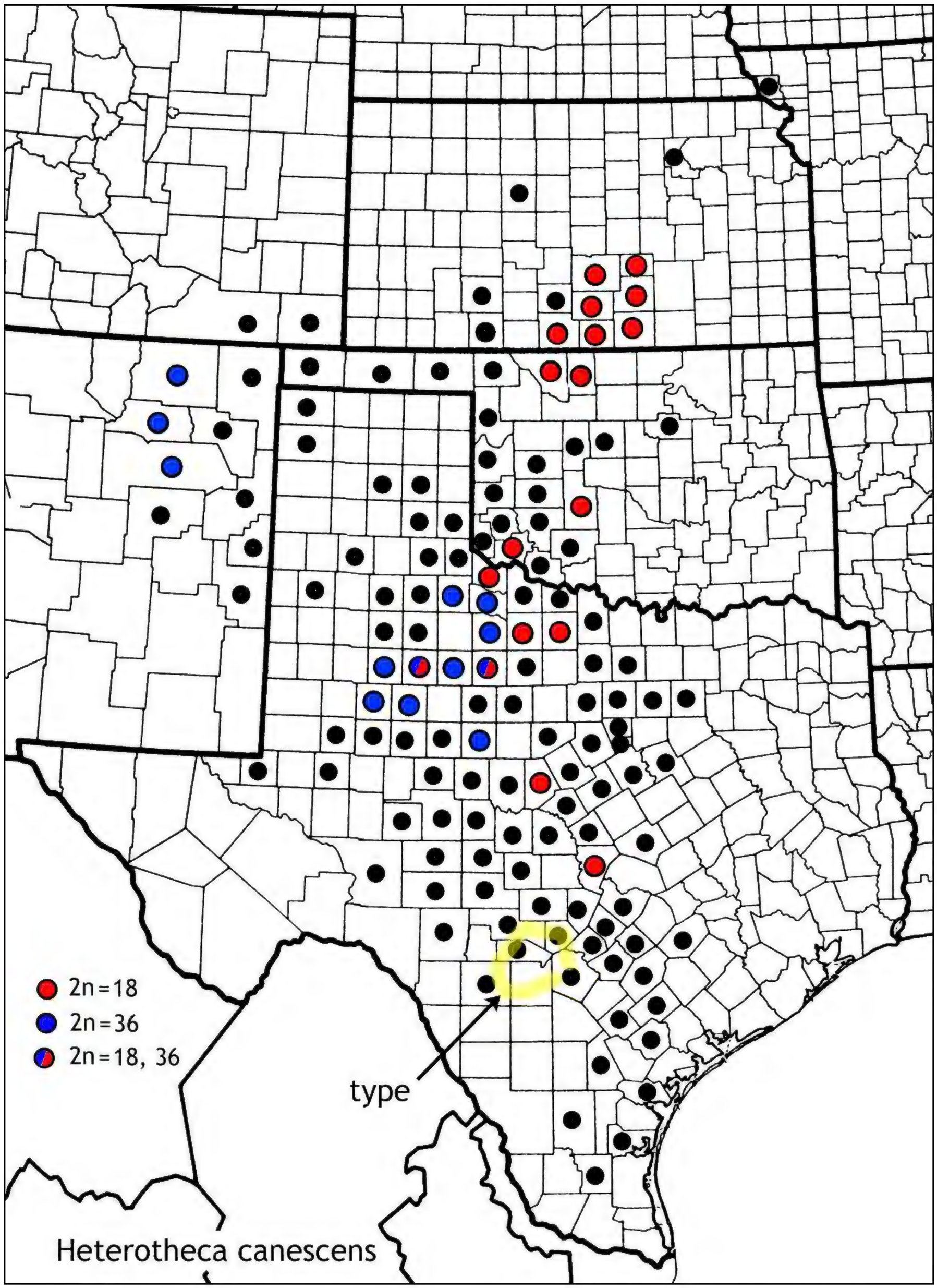
Map 3. Distribution of *Heterotheca vespertina* and *H. villosa*.



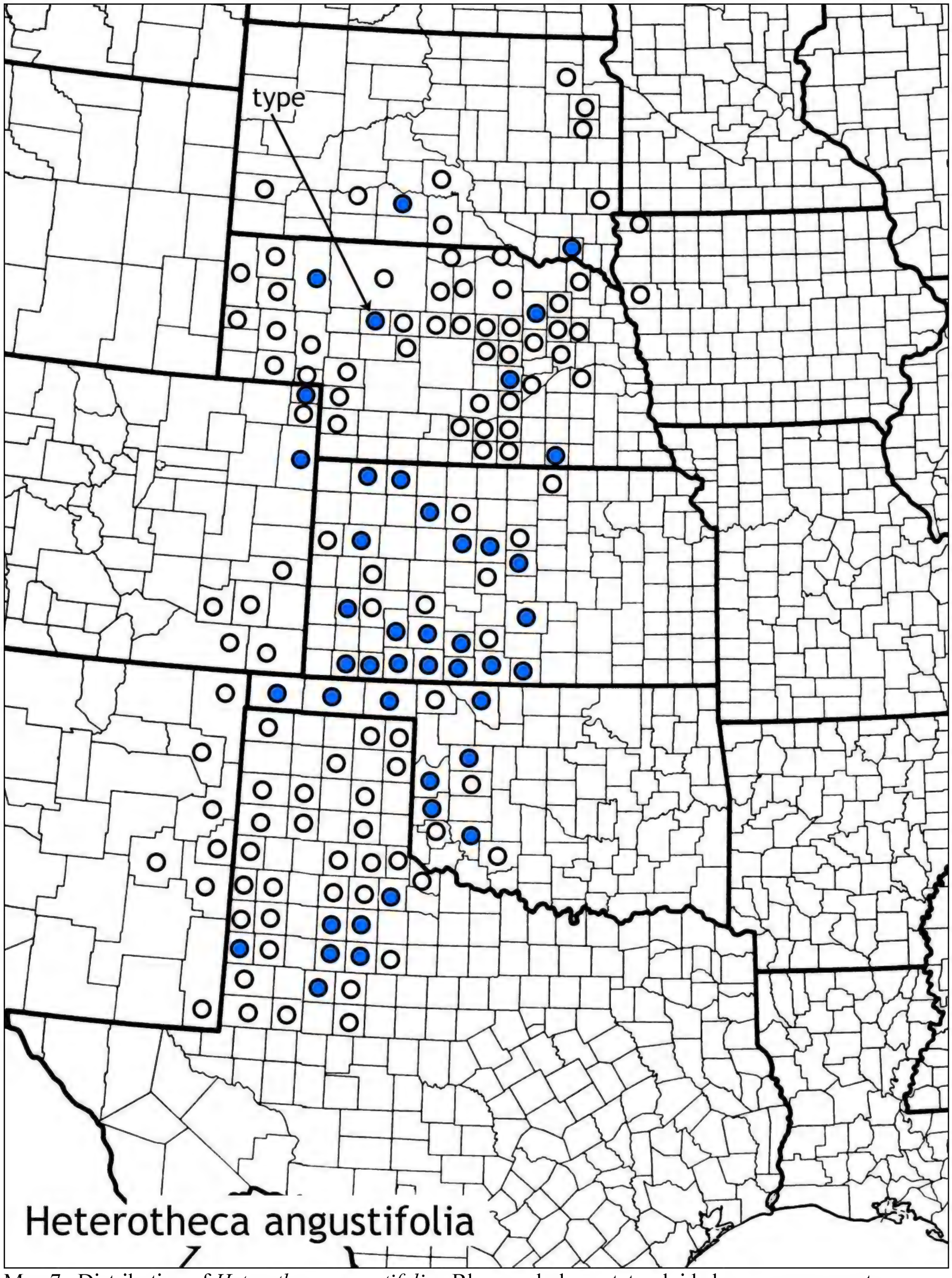
Map 4. Distribution of *Heterotheca orovillosa*.



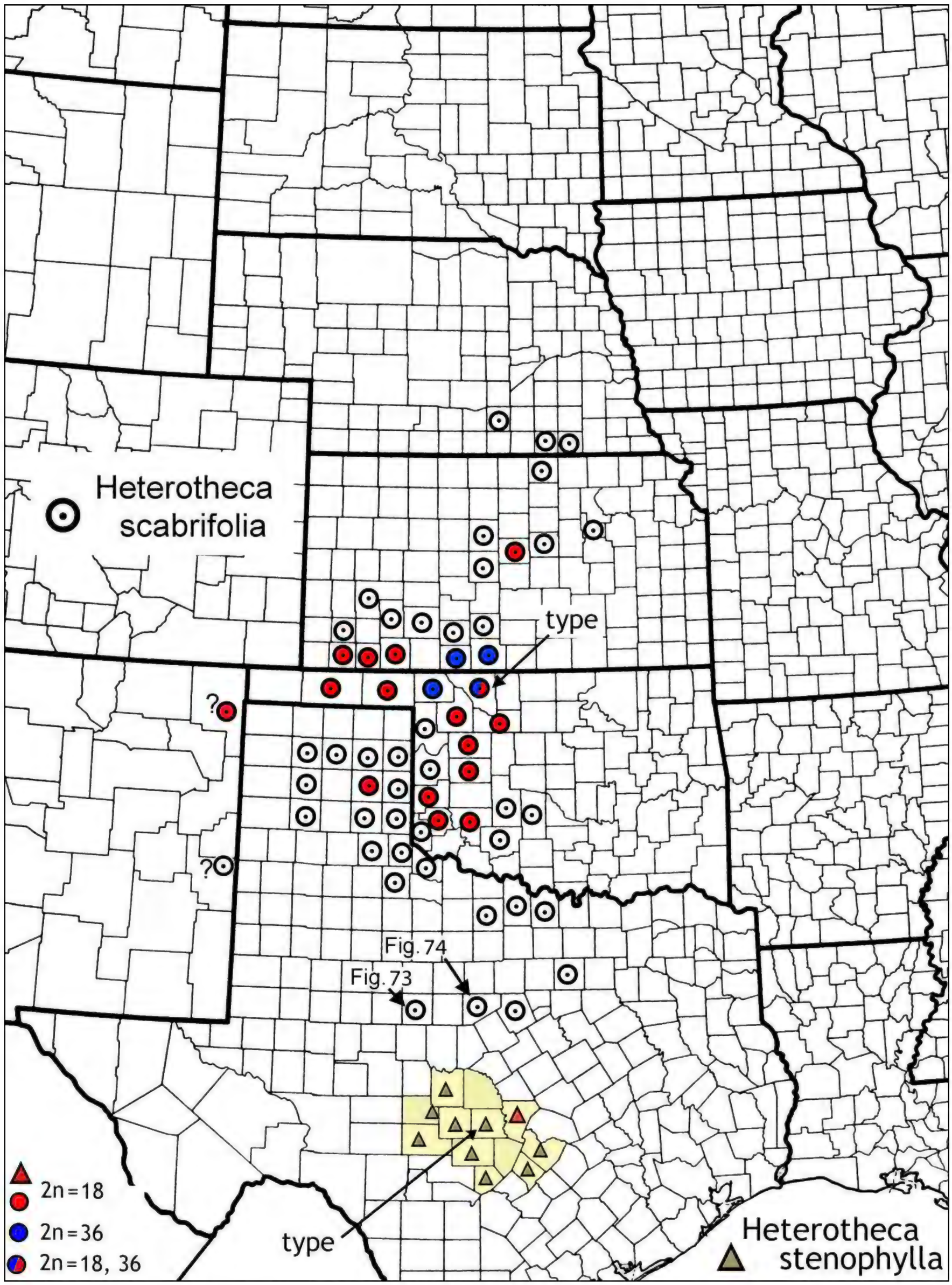
Map 5. Distribution of *Heterotheca* species. Names with arrows point to the type locality for *H. ballardii* and to type localities for *H. hispida* and synonyms.



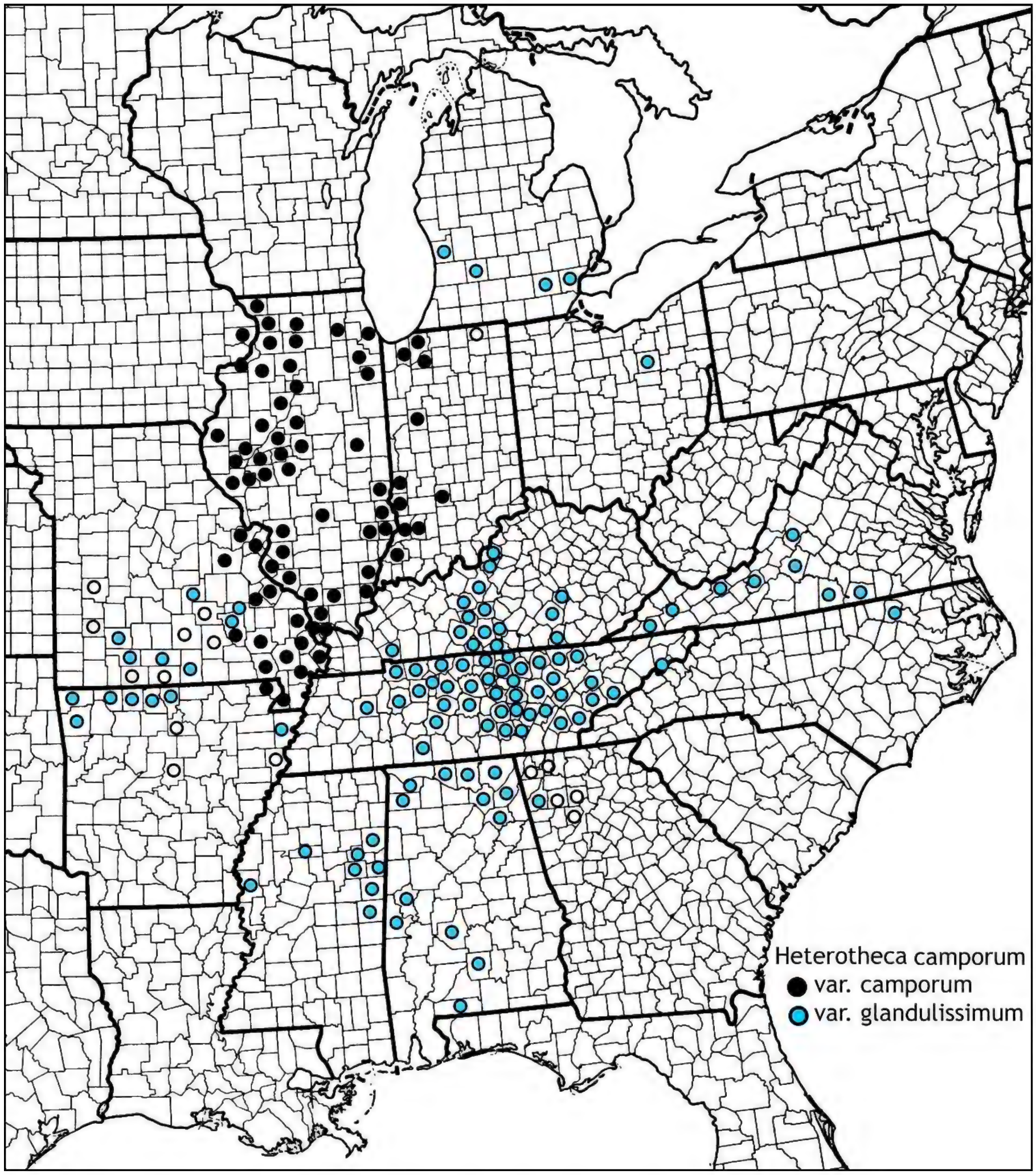
Map 6. Distribution of *Heterotheca canescens*. Yellow highlight outlines the route of Berlandier's 1828 trip — the type collection was made somewhere along his route



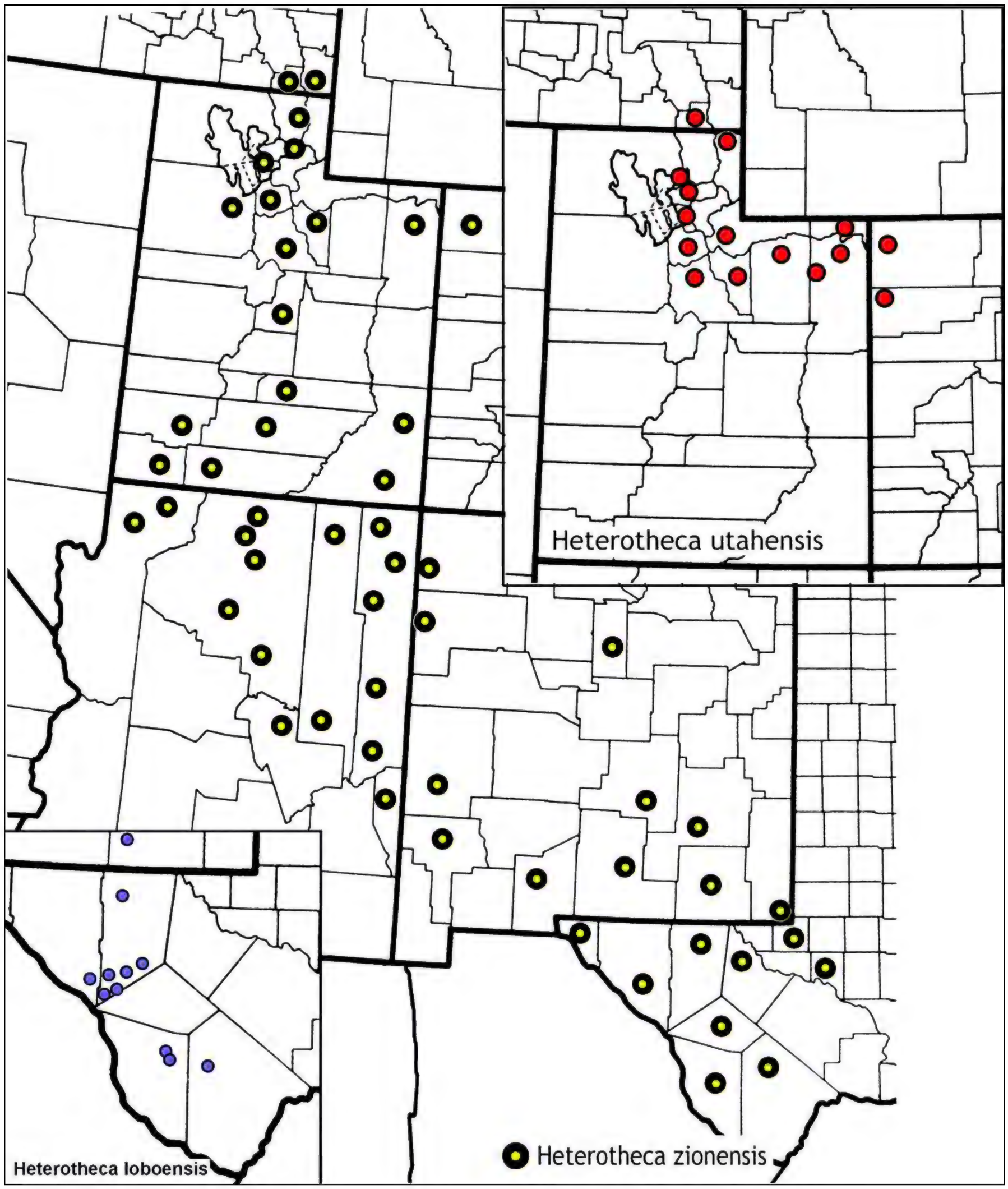
Map 7. Distribution of *Heterotheca angustifolia*. Blue symbols are tetraploid chromosome counts..



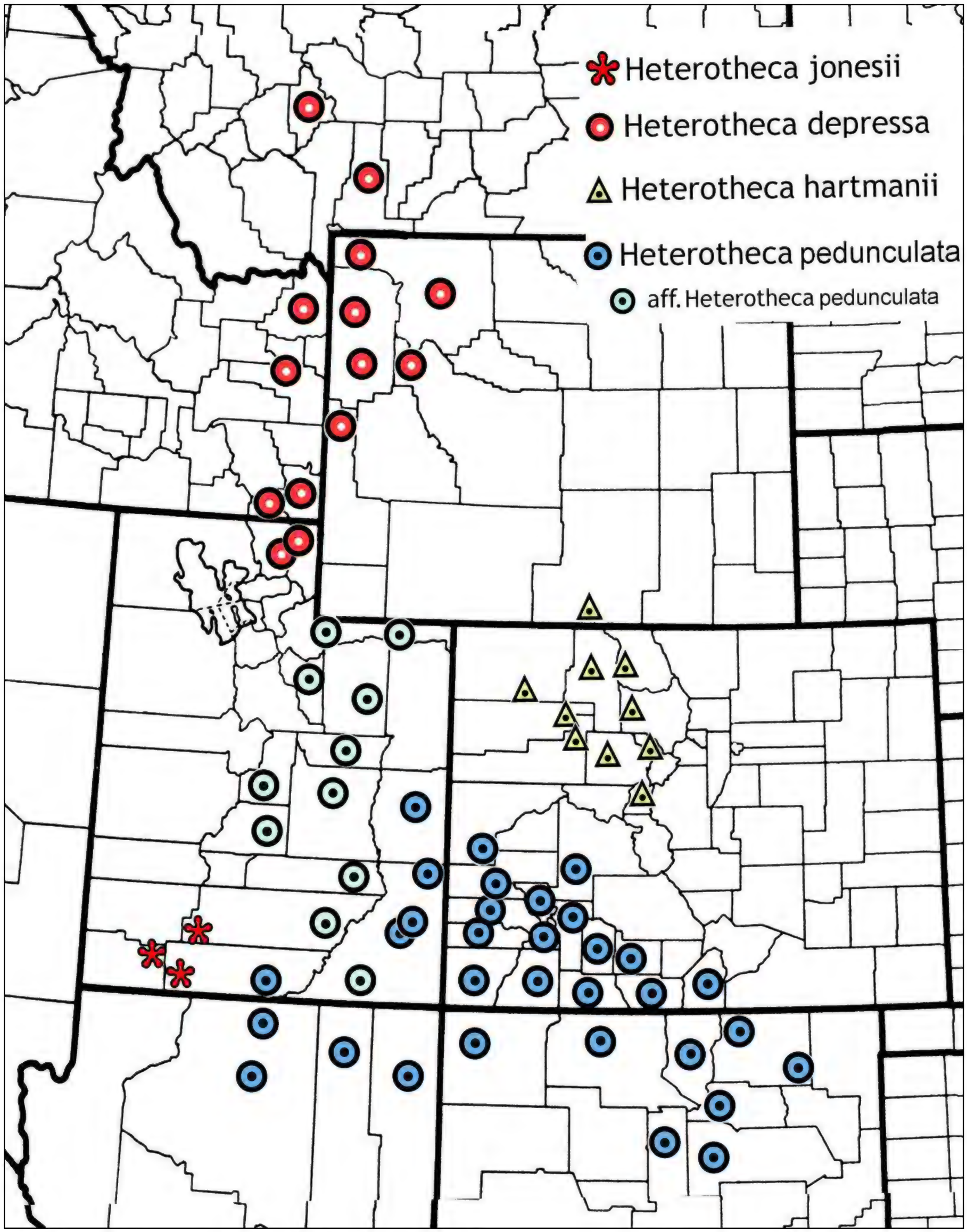
Map 8. Distribution of *Heterotheca stenophylla* and *H. scabrifolia*. Yellow highlight emphasizes the restricted geographic range of *H. stenophylla*. Putative morphological intermediates (see text) are illustrated in Figs. 73 and 74. Vouchers for New Mexico localities have not been seen in the present study (see text).



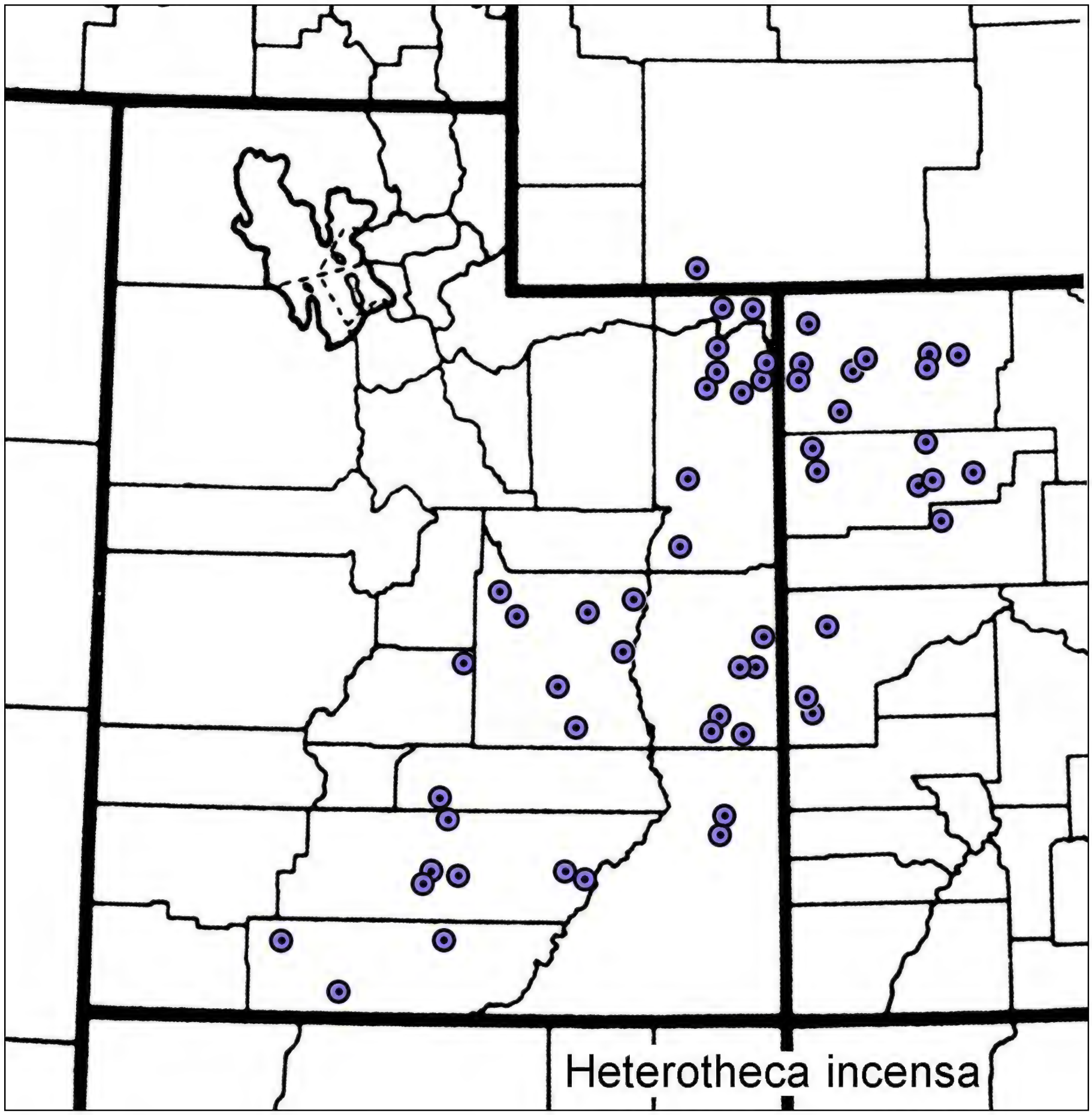
Map 9. Distribution of *Heterotheca camporum*. Vouchers not seen for unfilled symbols.



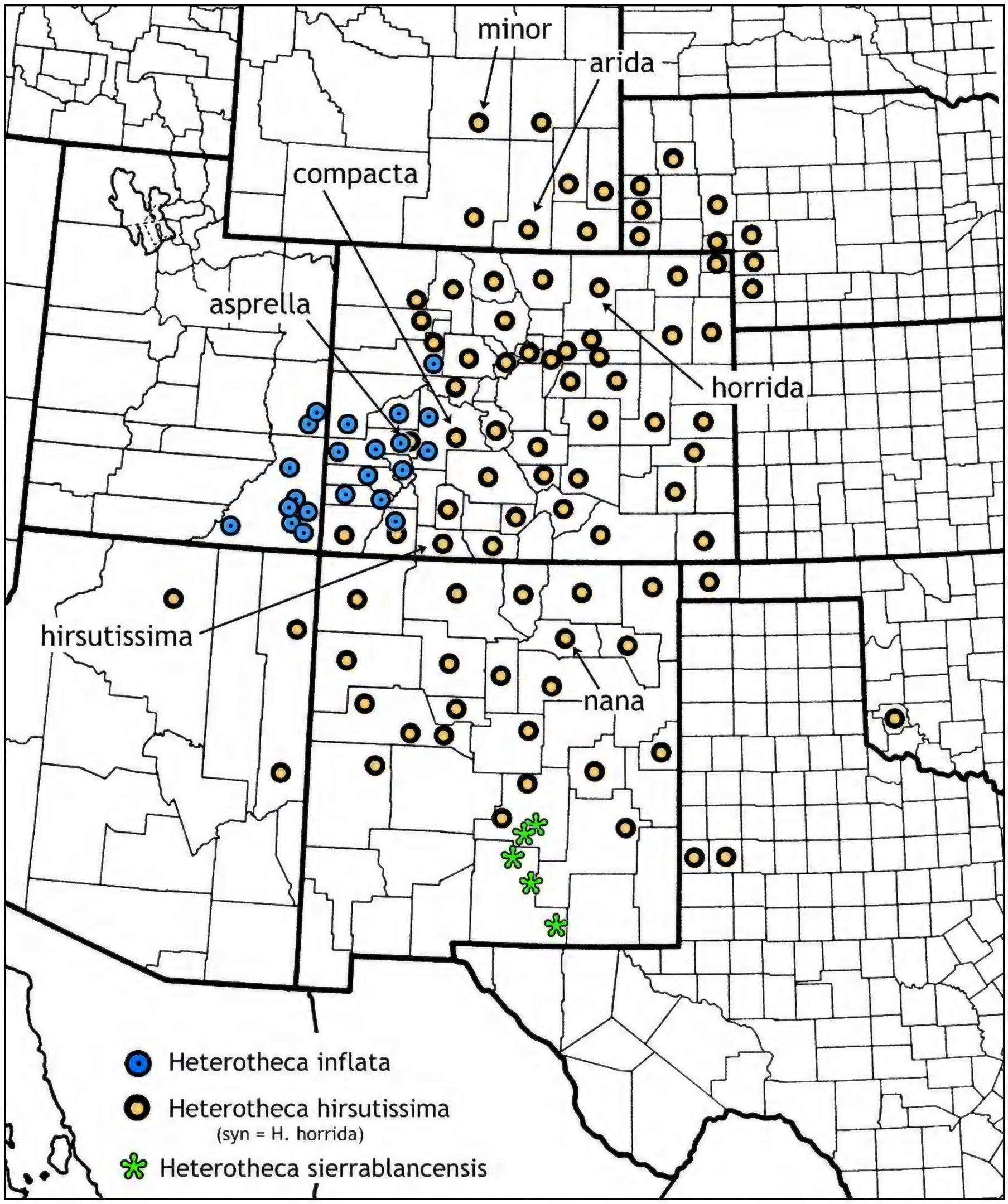
Map 10. Distribution of *Heterotheca zionensis*, *H. utahensis*, and *H. loboensis*.



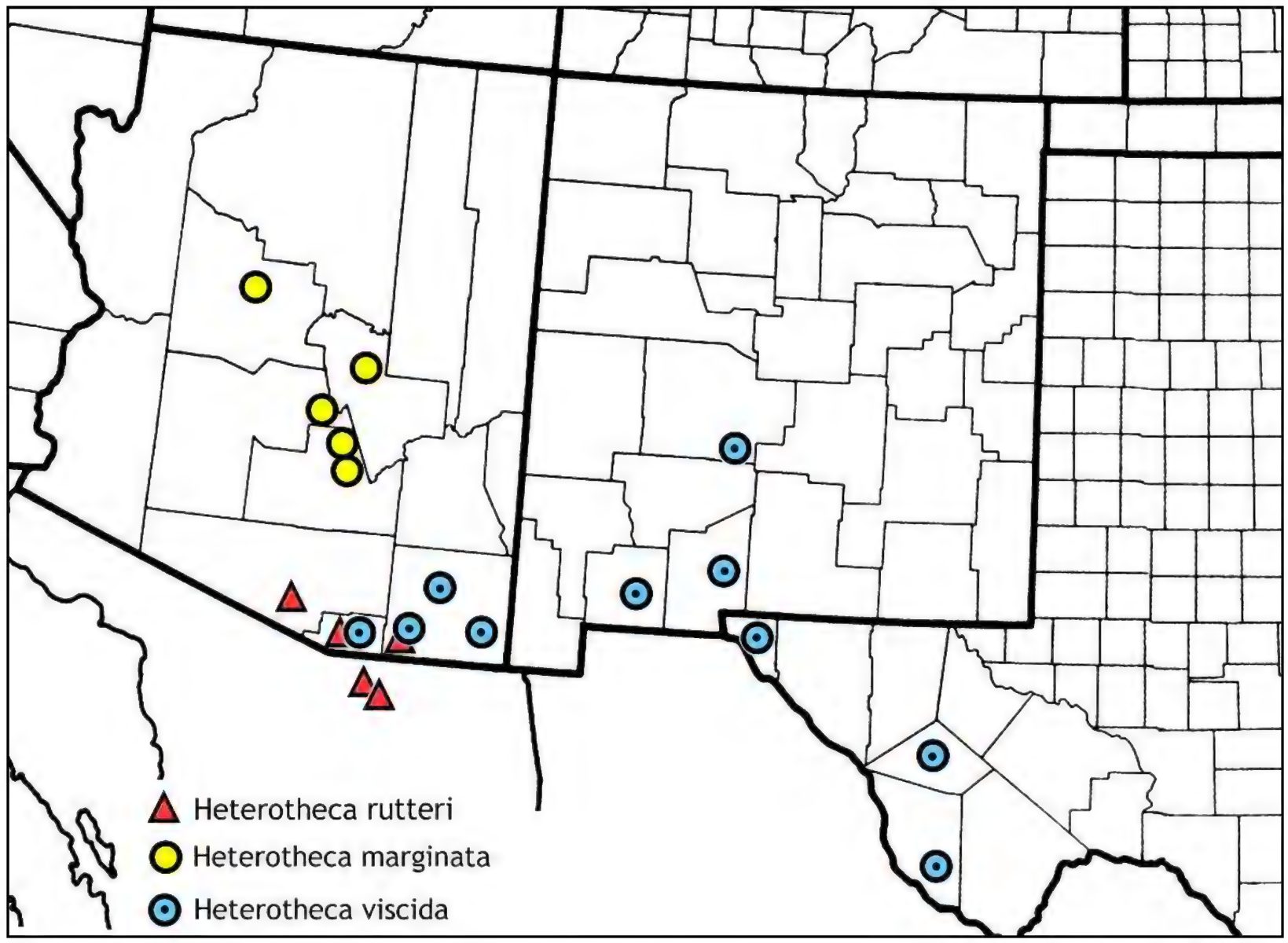
Map 11. Distribution of *Heterotheca* species. Symbols for *H. pedunculata* with lighter blue perhaps are a different species, yet undescribed. Also see text for comments on the "Uncompahgre variant" of *H. pedunculata*.



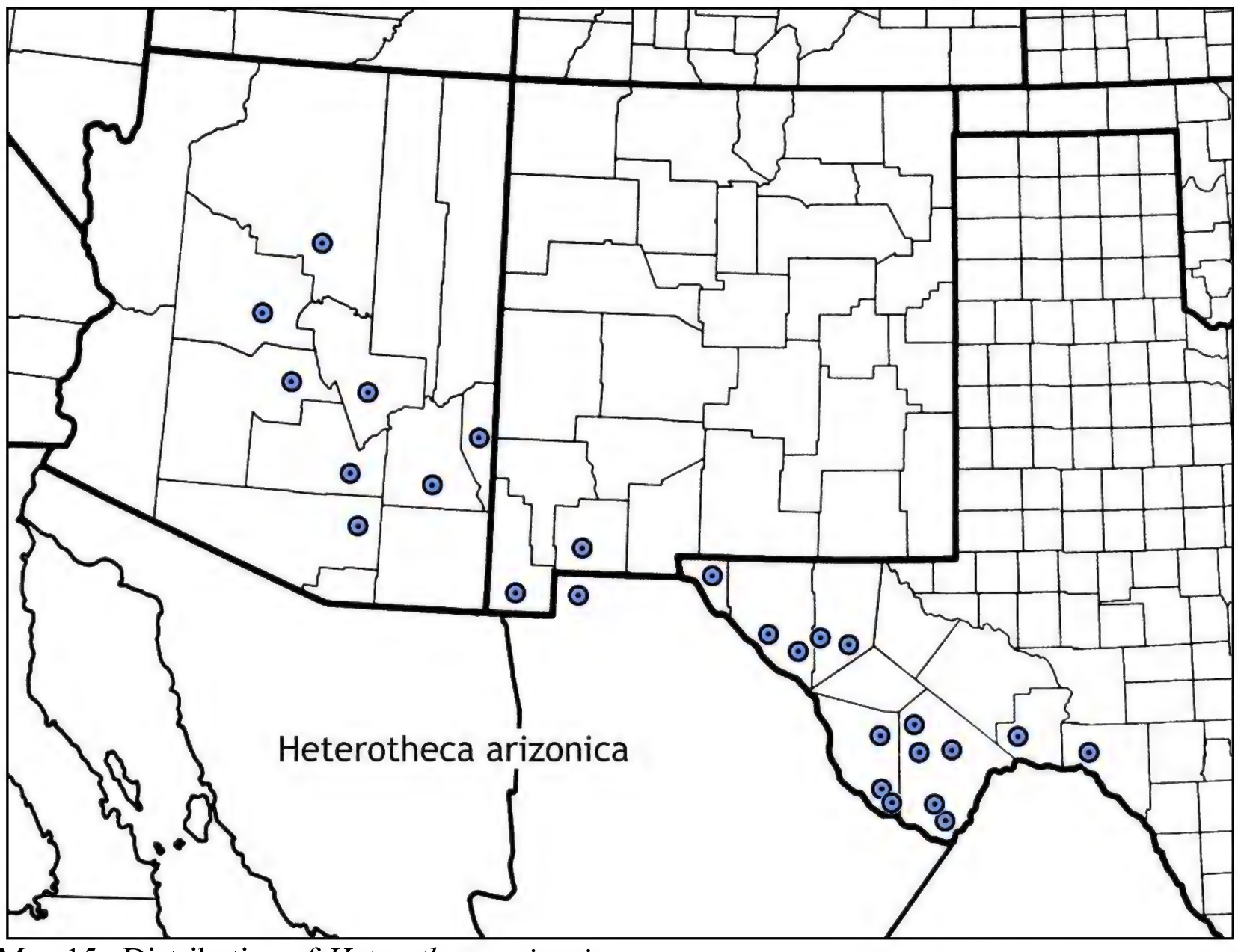
Map 12. Distribution of *Heterotheca incensa*.



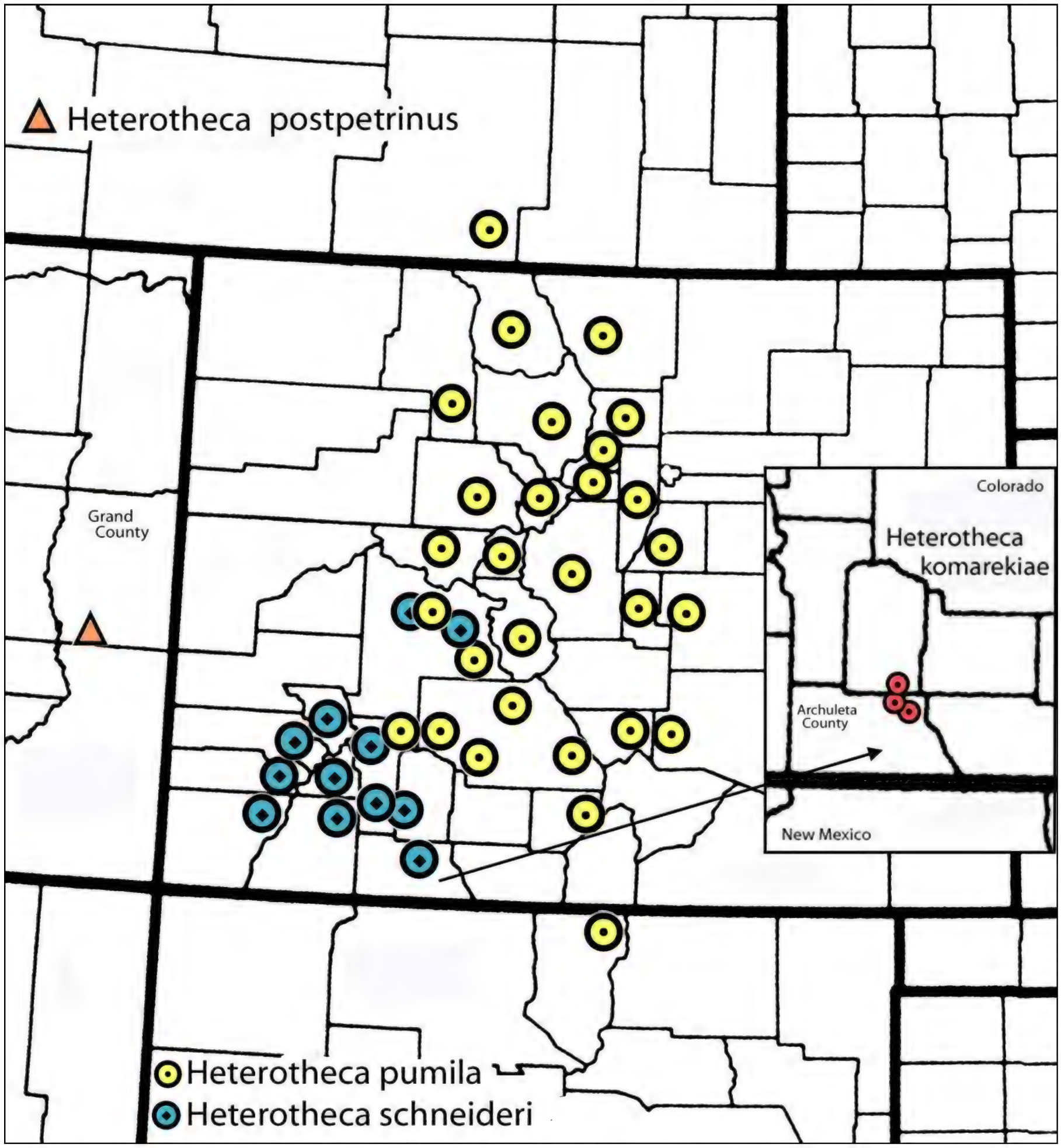
Map 13. Distribution of *Heterotheca* species. Names with arrows are types for *H. hirsutissima* and its synonyms. See text for comments on the disjunct locality in Oklahoma.



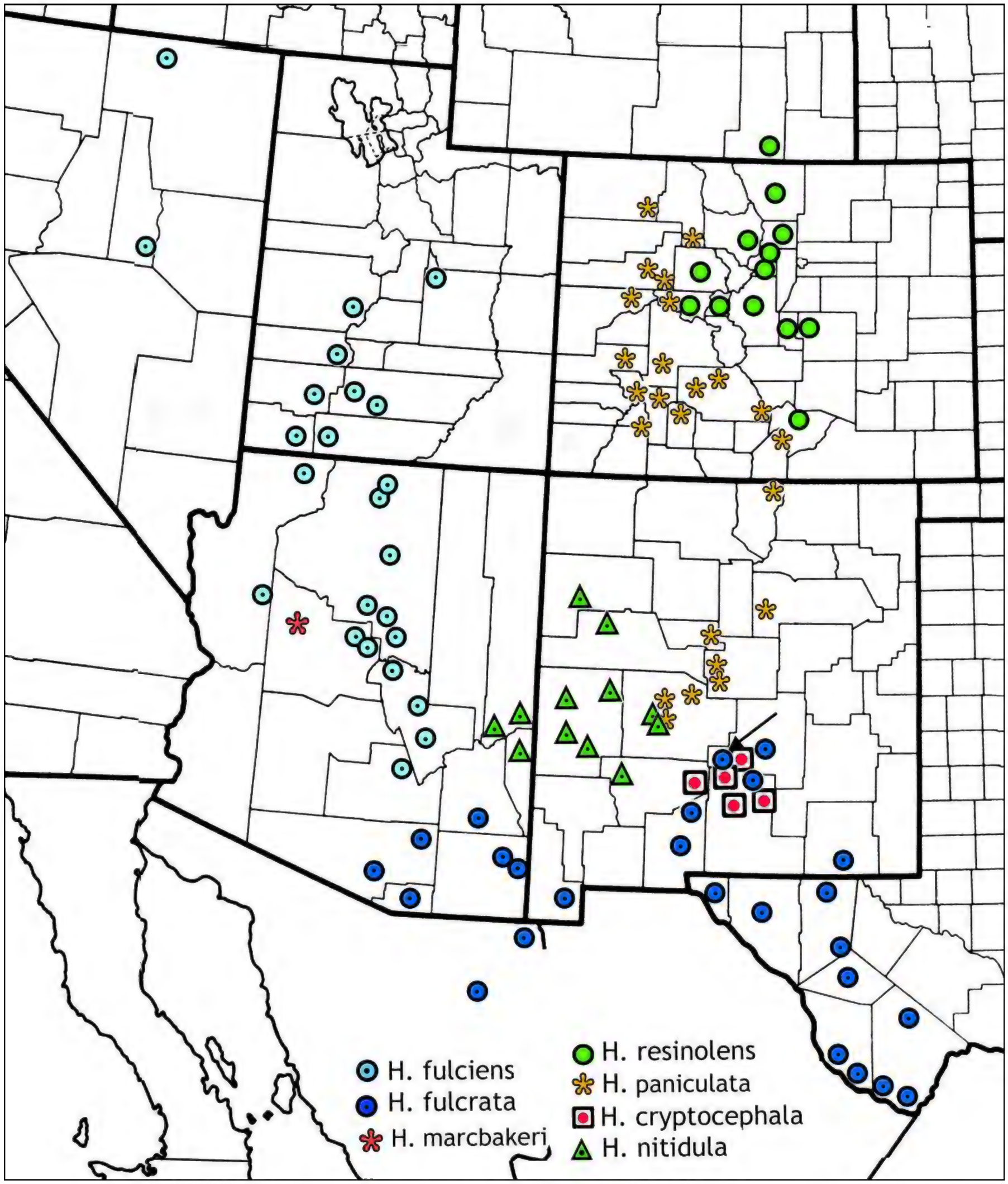
Map 14. Distribution of *Heterotheca rutteri*, *H. marginata*, and *H. viscida*.



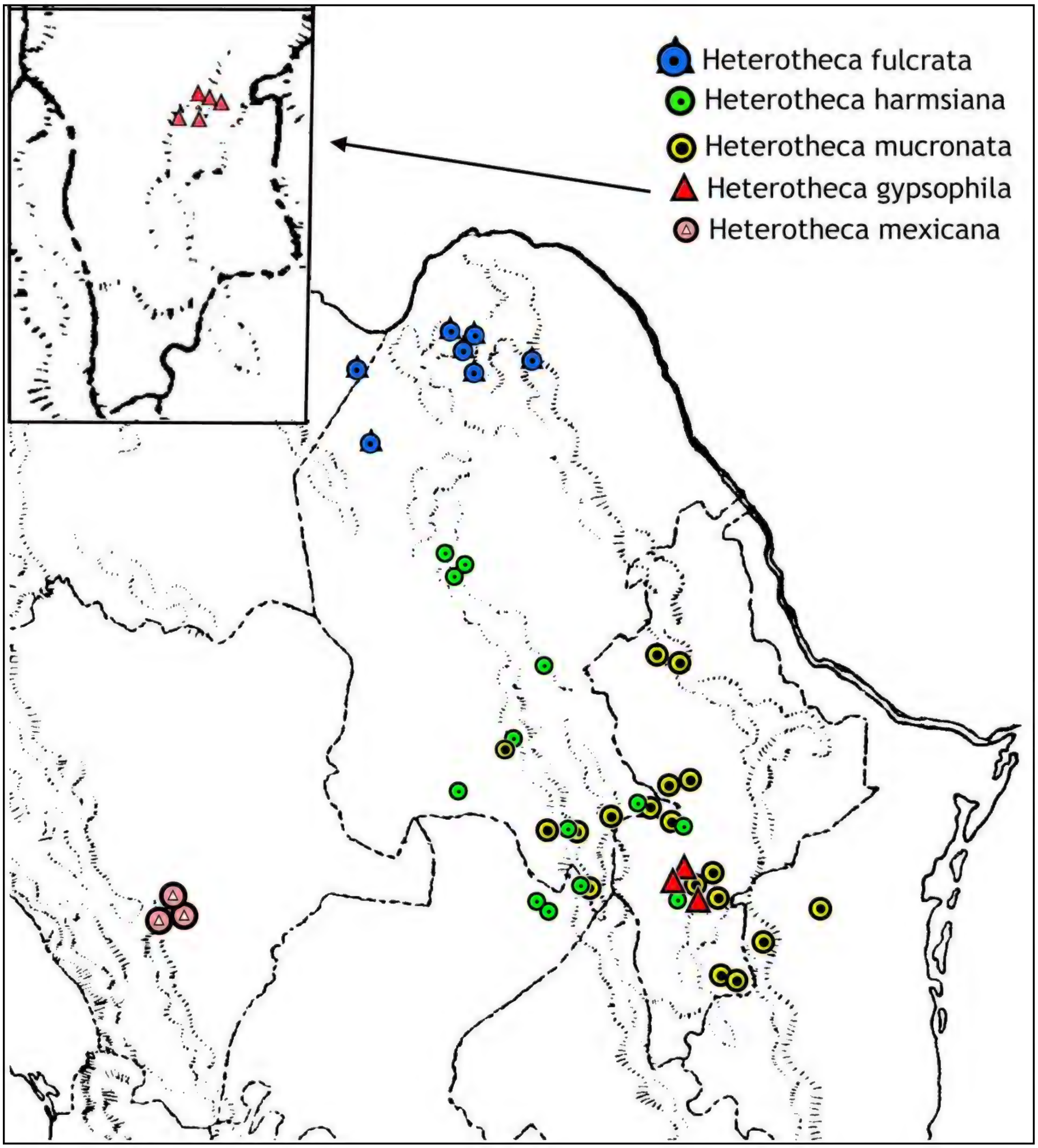
Map 15. Distribution of *Heterotheca arizonica*.



Map 16. Distribution of *Heterotheca pumila*, *H. schneideri*, *H. komarekiae*, and *H. postpetrinus*.



Map 17. Distribution of *Heterotheca* species. Arrow points to the type locality of *H. fulcrata*.



Map 18. Distribution of *Heterotheca* species. The range of *H. fulcrata* in the USA is shown in Map 17.

HETEROTHECA SECT. CHRYSANTHE Nesom **TYPE**: *Heterotheca villosa* (Pursh) Shinners

1. HETEROTHECA POLOTHRIX Nesom, Sida 22: 373. 2006 [as nom. et stat. nov.]. *Chrysopsis villosa* var. *scabra* Eastw., Proc. Calif. Acad. Sci. 2.6: 294. 1896. *Heterotheca villosa* var. *scabra* (Eastw.) Semple, Phytologia 73: 453. 1992. **TYPE**: **Utah**. San Juan Co.: Willow Creek, 14 Jul 1895, *A. Eastwood 38* (holotype: CAS image!). Not *Heterotheca scabra* (Pursh) DC. 1836 = *H. subaxillaris*.

Stems and leaves usually distinctly green from reduced non-glandular vestiture. **Stems** erect, usually little branched until distal 1/3, prominently sessile-glandular, loosely strigose to hirsute-strigose, hirsute-villous, or hirsute, sometimes essentially without non-glandular hairs. **Leaves** relatively widely spaced, usually ascending, oblong to oblong-lanceolate to oblanceolate, distal lanceolate to triangular-lanceolate, acute at apex, surfaces moderately to densely sessile-glandular, the glands little obscured by the sparsely strigose (nonglandular) vestiture, non-glandular hairs often less dense abaxially, often restricted to midvein area (middle 1/3) of adaxial surfaces, or sometimes nearly absent on both surfaces. **Heads** characteristically solitary on unbranched stems or appearing solitary on long, sparsely reduced-bracteate peduncles 2–5(–10) cm, sometimes few in a loosely corymboid arrangement when peduncles shortest; involucres 10–13 mm wide; phyllaries sparsely to moderately strigose, eglandular or minutely sessile-glandular, not viscid. **Ray flowers** 12–27. **Chromosome number**, 2*n*=36 (*Semple & Heard 7895*, *Semple 8817, 8819, 8823, 8827, 8828, 8897*, from Arizona, Colorado, and Utah).

Considerable variation occurs, but the characteristic form of the species occurs over the whole range. In northeastern Arizona, San Juan Co., Utah, and southwestern Colorado, stem vestiture of *Heterotheca polothrix* sometimes is antrorsely oriented and leaves have denser non-glandular vestiture, perhaps reflecting genetic influence of *H. pedunculata*. Some variants suggest gene exchange with *H. hirsutissima* where sympatric in the 4-Corners area.

In 2006, I included two species in the concept of *Heterotheca polothrix*, the typical expression (as in the present study) and *H. cinerascens* (recognized here as a distinct species). Semple (1987) first recognized the 'cinerascens' plants as distinct (as *H. horrida* subsp. *cinerascens*, from "western Utah and Nevada") but later (1996) included them as part of *H. villosa* var. *scabra*. The ranges of *H. cinerascens* and *H. polothrix* overlap slightly in southwestern Utah.

a. Phyllaries glandular or mostly eglandular, sparsely strigose with non-glandular hairs; cauline leaves commonly widely spaced, ascending, grading gradually into peduncular bracts; heads usually solitary on long, sparsely reduced-bracteate peduncles or few in a loosely corymboid arrangement; leaves often with adaxial and abaxial surfaces distinctly different in vestiture, the adaxial more densely glandular and less densely hirsute-strigose ..... 1. **Heterotheca polothrix**

a. Phyllaries completely glabrous or minutely glandular and resinous-viscid, without non-glandular hairs; cauline leaves and bracts often closely spaced, often overlapping, commonly spreading to deflexed, usually abruptly reduced and becoming bracteate distally; heads usually numerous in a corymboid arrangement, peduncular bracts characteristically continuing to immediately below heads; leaves densely and evenly sessile-glandular on both surfaces ..... 3. **Heterotheca cinerascens**

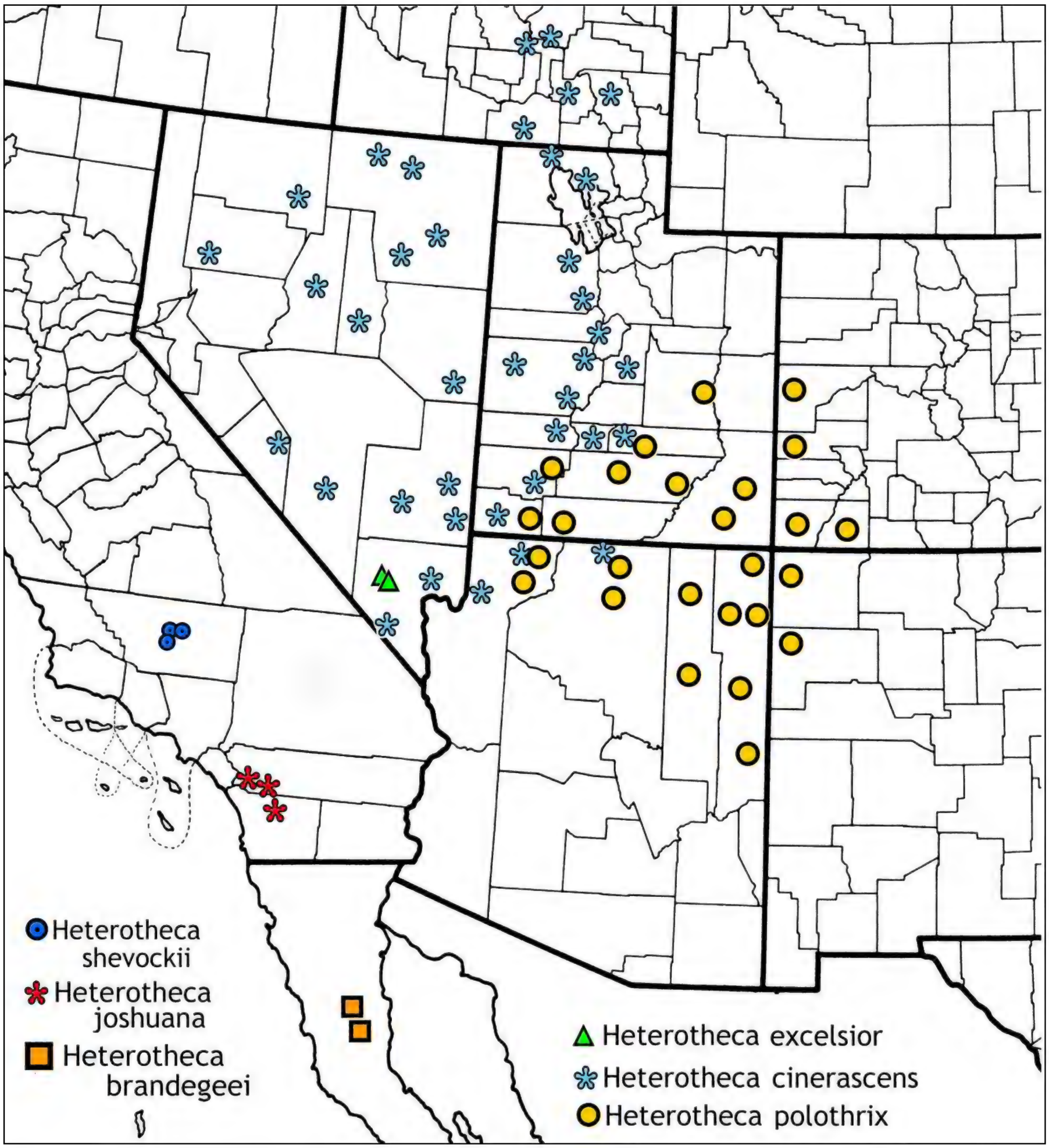


Figure 1. Distribution of *Heterotheca shevockii*, *H. joshuana*, *H. brandegeei*, *H. excelsior*, *H. cinerascens*, and *H. polothrix*.

Figure 2. *Heterotheca polothrix*, holotype (= *Chrysopsis villosa* var. *scabra*).

Figure 3. *Heterotheca polothrix*, McKinley Co., New Mexico.

Representative collections examined. **Arizona**. Apache Co.: Carrizo Mts, E. slopes, White Silver Mine Road, 7000-7500 ft, 26 May 1990, *Clifford AC-49* (BRY); Canyon de Chelly Natl Monument, 5700 ft, 13 Sep 1955, *Demaree 38385* (SMU); Hubbel Trading Post, Ganado, scattered across irrigation fields and ditches, 6300 ft, 2 Jul 1986, *Gandhi 220* (BRIT). Coconino Co.: Colorado River, Lees Ferry, River Mile 0, 2 May 1976, *Arnott 1994* (BRIT); Vermilion Cliffs Natl Monument, headwaters of Soap Creek above Cliff Dweller's Lodge, desert shrub, 6372 ft, 21 May 2003, *Atwood et al. 29266* (BRY); Navajo Mtn, 8000 ft, *Clute 38* (RM); San Francisco Mts near Clifton, 1 Nov 1880, *Greene 12856* (MO); Vermilion Cliffs Natl. Mon., 1570 m, 16 Jun 2003, *Higgins & Atwood 24673* (BRY); N side of Lee's Ferry, sandstone crevices, 7 Jul 1927, *Jaeger s.n.* (POM); 50 mi S of Lee's Ferry, 12 Jun 1890, *Jones s.n.* (POM); Grand Canyon, 7000 ft, 28 Jun 1898, *MacDougal 177* (RM); Cape Royal, N side of Grand Canyon, 7876 ft, 15 Jul 1927, *Peirson 7420* (RSA); halfway between Cameron and Desert View, Hwy 64, 15 Oct 1937, *Ramsey 2857* (RSA); 9.6 km E of Jacob Lake on US 89-Alt, pine woods, 12 Sep 1985, *Semple & Heard 7895* (MO). Mohave Co.: Near Robinson reservoir, T36N, R5W, S21, 12 Jun 1979, *Coombs & Bundy 2826* (BRY); Cottonwood Spring, T42N, R6W, S34, 5 Oct 1978, *Gierisch 4548* (BRY); Grand Canyon NP, Twin Springs Canyon, Redwall Narrows, beginning of perennial flowing water, 3080 ft, 28 Aug 2008, *Rink 8126* (BRY). Navajo Co.: 3.0 mi W of Boot Mesa, unnamed canyon drainage from N Todicheenie Bench, base of sandstone walls and talus slopes, 5600 ft, 23 Sep 2001, *Clifford & Heil 01-1314* (BRY); Holbrook, 18 Aug 1896, *Zuck s.n.* (MO). **Colorado**. La Plata Co.: ca. 10 mi N of Durango along US 550, ca. 2020 m, 24 May 2000, *King & Garvey 11292* (BRIT, MO, NY). Mesa Co.: Ca. 5 air mi NE of Gateway, dry wash and adjacent hillsides, pinyon-juniper, 5500 ft, 16 May 1994, *Lyon 3150* (RM); Gateway Nature Area N of Gateway between Colo Hwy 141 and Dolores River, base of N-facing Wingate cliff, 30 Aug 2010, *Yeatts 5953* (BRY, COLO, KHD). Montezuma Co.: Mesa Verde Natl Park, 8 Jul 1929, *Mathias 639*, mixed with *H. pedunculata* (PH). Montrose Co.: Western Montrose Co., bedrock, 5000 ft, 14 Jul 1924, *Payson 3922* (RM). **New Mexico**. McKinley Co.: Mesa between Peach Spring and Red Mesa canyons, rolling hills, sandy soil, ca. 6700 ft, 10 Sep 1976, *Wagner 2017* (UNM image!). San Juan Co.: 3 mi E of Farmington, alluvium of San Juan River, 31 Aug 1961, *Cannon s.n.* (UNM). **Utah**. Emery Co.: 10 mi W of Greenriver along I-70, roadside, 4700 ft, 11 Sep 1986, *Atwood 12432* (NY); Range Creek Canyon, ca. 0.7 road mi S of jct of Turtle Canyon and Range Creek roads, sandy loam with *Tamarix* and *Populus*, 4660 ft, 29 Jun 2007, *RCC 2007-27* (UT). Garfield Co.: 18 mi S of Notom Hwy 24 jct and ca. 2 mi N of Cedar Mesa Camp Ground road, pinyon-juniper, 1700 m, 15 Jun 1991, *Atwood 15588* (ID-2 sheets); ca. 3 mi N of Bakers Ranch, large side canyon just S of Millers Canyon in Halls Creek drainage, 4000-4500 ft, 30 May 1977, *Camp 25* (WTU); jct Calf Creek and Escalante River, sandy soil, 6000 ft, 21 Jun 1957, *Cottam 14687* (WTU); N of Escalante, sandy draw, 5900-6100 ft, 19 Jun 1938, *Pennell & Schaeffer 21963* (PH). Utah Hwy 95, vicinity of Hog Spring picnic area, just W of Glenn Canyon Natl Rec. Park, washes and ditches, 16 Jun 1987, *Semple 8819* (MO); Utah Hwy 12, 1 km S of Boulder, cracks in checkerboard sandstone, 16 Jun 1987, *Semple 8823* (MO); N of Escalante on Hells Backbone Bridge road, extensive rock outcrop below and E of road, common in sandy pockets, 16 Jun 1987, *Semple 8827* (BRIT); ca. 0.5 km NW of Hell's Backbone Bridge, ponderosa pine, 18 Sep 1987, *Semple 8899* (MO). Iron Co.: Cedar Breaks, dry meadow, 10,000 ft, 17 Jul 1930, *Goodman & Hitchcock 1618* (DS). Kane Co.: Side branch of Clear Creek ca. 2 mi N of East Entrance to Zion Natl Park, 6200 ft, 21 Jun 1979, *Ertter 2871* (WTU); along Colorado River, 2 mi below and on opposite side from Lake Creek, Shock Trail Bar, 18 Apr 1957, *Gaines 841* (WS); 0.5 km E of E boundary of Zion Natl Park, 17 Jun 1987, *Semple 8828* (MO); Clay Creek, dry hillsides, 8100 ft, 11 Aug 1927, *Taylor T-11* (RM); 1 mi S of Hwy 89 on hill of Chinley Fm, pinyon-juniper, 1600 m, 10 May 1992, *Thorne & Zupan 10134* (BRY, RM). San Juan Co.: Canyon No. 2, 1936, *Buss s.n.* (RSA); 8 mi N of Blanding, dry creek bed, 22 Jun 1938, *Cutler 2348* (MO); 4 mi W of Blanding, among pinyons, 5600 ft, 11 Sep 1939, *Cutler 3044* (SMU); Navajo Mts, Navajo Indian Reservation, ca. 40 air mi NE of Glen Canyon Dam, ponderosa pine, 8200 ft, 3 Aug 1967, *Gentry 1787* (ID! image!, SMU, WTU); Roan Bailey Mesa, ca 22 mi N of Monticello, 26 May 1986, *Grimes 2950* (MO); 30 mi SSE of Moab, E of US 163 near Lisbon Valley, just W of Big Indian Valley, W-facing dip slopes on carbonate cemented sandstone and mudstones, 6000-7000 ft, Jul 1984, *Jones 21* (BRIT); Sierra La Sal, 5-6000 ft, May-Oct 1899, *Purpus 7017* (MO); SW of Blanding, 2.1 km W of US Hwy 191 on Utah Hwy 95, cliff face of road cut, 16 Jun 1987, *Semple 8817* (MO). Wayne Co.: Fruita, sandy slopes, 4500 ft, 2 May 1944, *Cottam 9279* (UT); Natural Bridge near Fruita, dry sandy wash,

7000 ft, 6 Apr 1934, *Harrison 7394* (KANU); ca. 5 mi N of Caineville, N Caineville Mesa, Emery sandstone, juniper-mtn mahogany, 6000 ft, 25 May 1986, *Kass 2295* (BRY, RM); Canyonlands Natl Park, Virginia Park, 11 Jun 1967, *Kleiner & Harper s.n.* (UT); Canyonlands Natl Park, Virginia Park, 8 Aug 1967, *Kleiner & Harper s.n.* (UT); Canyonlands Natl Park, Virginia Park Canyon, 8 May 1968, *Kleiner & Harper s.n.* (UT); near Capitol Reef Natl Monument, 10 mi SSE of Fruita, sandy soil in steep narrow canyon, 1500-1650 m, 9 Jun 1953, *McVaugh 14531* (SMU, VDB); ca 5 km S of Grover on Utah Hwy 12, 7900 ft, 18 Sep 1987, *Semple 8897* (BRY, MO); San Raphael Desert, sandy wash, 4500 ft, 7 Jul 1930, *Stanton 494* (UT); Capitol Reef Natl Monument, along meadows and orchards of Robber's Roost Farm, 5400 ft, 18 May 1956, *Vickery 571* (UT). Washington Co.: Zion Natl Park, valley floor of Zion Canyon near visitor center, pinyon-juniper, dry rocky slopes, 3800 ft, 15 Aug 1986, *Charlton 526* (OBI); Zion Natl Park, Zion Canyon, 1-3 Aug 1925, *Pilsbry s.n.* (PH).

2. HETEROTHECA EXCELSIOR Nesom, **sp. nov. TYPE: Nevada**. Clark Co.: Charleston Mts [= Spring Mts], Excelsior Canyon, sandy soil with *Pinus scopulorum*, *Salix*, 1200 m, 7 Sep 1941, *Clokey 8759* (holotype: MO 1293502!; isotypes: BRY-3 sheets!, CAS!, CM fide Seinet, CS fide Seinet, DS!, IDS-Fig. 6, LL!, MO-1293502!, NY-2 sheets!, PH-2 sheets!, POM!, RM-2 sheets!, SMU!, TENN-Fig. 5, TEX!, UC!, VDB!, WTU-2 sheets!).

Recognized by its long, unbranched, eglandular and loosely strigose stems, gradually reduced cauline leaves, and relatively small heads in a corymboid panicle. Similar to *Heterotheca polothrix* and *H. cinerascens* in its relatively large heads, eglandular stems, leaves glandular on both surfaces and with reduced non-glandular vestiture adaxially, and its southwestern USA geography. Similar to *H. polothrix* in its few-branched stems (below the inflorescence) but distinct in its branched inflorescence (vs. few-headed inflorescence), shorter stem vestiture, denser and finely strigose, non-glandular leaf vestiture (vs. hispid to hispid-hirsute or strigose-hirsute), and more densely imbricate phyllaries (vs. phyllaries in 3–4 series). Distinct from *H. cinerascens* in its non-glandular stem vestiture, ascending branches (vs. stiffly spreading) and rigid leaves, strigose phyllaries (vs. glandular, completely without non-glandular hairs), densely short-strigose leaf vestiture (vs. glandular and sparsely strigose or non-glandular hairs absent), lack of capitular bracts, and leaf apices without an indurate apiculum.

Stems apparently stiffly erect, 50–80 cm, unbranched until the distal 1/4–1/5, without axillary buds, loosely strigose to puberulent-strigose with upward-arching hairs, eglandular. **Leaves** (only cauline observed) oblong-oblanceolate to oblong-elliptic or lanceolate, not twisted, gradually reduced in size upward, closely ascending to spreading, mid cauline 2–35 x 4–6 mm, longest (proximal) to 40 x 9 mm, bracteate in the inflorescence, surfaces finely and densely strigose with short, thin-based hairs, more densely so abaxially, densely and minutely sessile-glandular on both surfaces, more conspicuously so adaxially, margins eciliate or with a few, spreading cilia at the very base. **Heads** in a compact to loose corymboid panicle; capitular bracts absent; involucres 6–9 mm wide (pressed), inner phyllaries 5–6 mm long, phyllaries loosely and finely strigose, glandular on a dark patch near the apex, imbricate in 4–5 series, linear-lanceolate, scarious-margined. Ray florets 10–21. The 24 sheets of the type collection include about 38 stems, all relatively consistent in morphology, but there is enough variation in vestiture and leaf shape and distribution to indicate that they were taken from more than a single plant.

Flowering Aug-Oct. Pine woods in sandy soil, rocky (sandstone) sites, ca. 1200 m. Apparently endemic to Red Rock Canyon National Conservation Area. Clokey's "Excelsior Canyon" refers to the site of a sandstone quarry operated by Excelsior Company, which operated between 1905 and 1912. All three known localities (including Willow Spring and Pine Creek Canyon) are in an area within a radius of 1.5–2 miles (Fig. 4).

Additional collection: Clark Co.: Spring Mts, common perennial in rocky sites about Willow Spring, ca. 4000 ft, 4 Oct 1968, *Niles 855*, NY, UT-2 sheets-Figs. 7 and 8). And see photo from Pine Creek Canyon, Figs. 9 and 10.

Figure 4. *Heterotheca excelsior* localities, Red Rock Canyon National Conservation Area, Clark Co., Nevada. Excelsior Canyon, *Clokey 8759* (the type); Willow Spring, *Niles 855*; Pine Creek Canyon, photo by Stan Shebs (see Figs. 9 and 10). Google Earth.

Figure 5. *Heterotheca excelsior*, isotype (TENN).

Figure 6. *Heterotheca excelsior*, isotype (IDS).

Figure 7. *Heterotheca excelsior*. Willow Spring area, in Red Rock Canyon National Conservation Area, Nevada. *Niles 855* (UT 119848).

Figure 8. *Heterotheca excelsior*. Willow Spring area, in Red Rock Canyon National Conservation Area, Nevada. *Niles 855* (UT 119847).

Figure 9. *Heterotheca excelsior*. Detail from Figure 10. Pine Creek Canyon in Red Rock Canyon National Conservation Area, Nevada. Photo by Stan Shebs, 4 May 2007; Wikimedia Commons.

Figure 10. *Heterotheca excelsior*. Pine Creek Canyon in Red Rock Canyon National Conservation Area, Nevada. Photo by Stan Shebs, 4 May 2007; Wikimedia Commons.

Over the course of this study, I annotated some sheets of *Clokey 8759* as *Heterotheca polothrix*, but the Spring Mountains locality is disjunct — west of the *H. polothrix* range — and it became clear that many features of these plants are not within the morphological spectrum of *H. polothrix*. The only other *Heterotheca* collections I have seen from Clark County are *H. cinerascens*, which is even more different than is *H. polothrix* (see diagnosis). *Heterotheca cinerascens* in typical form grows in the Spring Mountains (e.g., *Jaeger s.n.*, *Pinzl 9868*), including the Red Rock Canyon area. Photographs (habit and details) of a goldenaster on red sandstone are typical *H. cinerascens* (www.Birdand Hike.com/Shrubs Around Las Vegas — Jim Boone).

Several UNLV collections (not seen) identified as *Heterotheca villosa* var. *villosa* from along Pine Creek in Red Rock Canyon National Conservation Area probably are *H. excelsior* — *Leary 592* and *3865*, *Fisher & Kennedy s.n.* These contrast with UNLV collections identified as *H. villosa* var. *hispida* from Clark County, including Red Rock Canyon NCA. *Pinzl 9868* from the Red Spring area of the Red Rock Canyon NCA is *H. cinerascens*.

3. HETEROTHECA CINERASCENS (Blake) Nesom, **comb. et stat. nov.** *Chrysopsis viscida* A. Gray subsp. *cinerascens* Blake, Proc. Biol. Soc. Washington 35: 173. 1922. *Heterotheca horrida* subsp. *cinerascens* (Blake) Semple, Brittonia 39: 381. 1987. **TYPE**: **Utah**. [Beaver Co.: fide Welsh 1982]: Beaver Creek Cañon, common among rocks, oak region, 2 Sep 1901, *I. Tidestrom 2873* (holotype: US image!; isotype: WIS image!).

A distinctive species, almost always in rocky habitats, characterized by sparsely to moderately puberulent-hirsutulous stems, stiff, sessile-glandular and otherwise sparsely and loosely strigose to hirsute-strigose, eciliate leaves, linear to linear-oblanceolate or narrowly lanceolate capitular bracts, and evidently keeled phyllaries sessile-glandular and often resinous but otherwise glabrous. **Stems** mostly 10–40 cm, mostly erect from the base. **Leaves** narrowly elliptic-oblanceolate to elliptic, (5)10–20(–30) mm wide, (1–)2–7 cm long, epetiolate, the distal cauline usually deflexed or at least spreading, often abruptly smaller, surfaces densely and evenly sessile-glandular, also sparsely to moderately hirsute to hirsute-strigose, vestiture sometimes more reduced adaxially. **Heads** numerous in a loosely corymboid arrangement, without capitular bracts; involucres (7–)9–11 mm wide, phyllaries linear-lanceolate, inner 5–7 nmm long. **Ray flowers** 10–17. Chromosome numbers, 2*n*=18 (*Semple & Heard 7818, 7876; Semple et al. 9270*), 2*n*=36 (*Semple & Heard 7857*).

Flowering (Jun–)Jul–Oct. Steep rocky slopes, among boulders, rock outcrops, cliffs, crevices, on limestone, granite, lava flows, and tuff; (rarely 3000–4000)4450–8200(–8850, rarely 9500–10,500) ft.

Additional and representative collections examined. **Arizona**. Coconino Co.: Vermilion Cliffs Natl Recreation Area, Navajo blow sand, pinyon-juniper-sagebrush community, 6061 ft, 13 Sep 2005, *Higgins 26873* [influence of *H. polothrix*?] (BRY); Vermilion Cliffs Natl Monument, Cathedral Wash, Upper Lowrey Spring, Navajo sandstone, high desert shrub, riparian, 4602 ft, 2 Aug 2012, *Hodgson 27296* (BRY). Mohave Co.: Parashant Canyon, sandy to gravelly canyon bottom, *Chrysothamnus-Brickellia-Acacia* community, 1100 m, 11 Oct 2000, *Higgins & Atwood 21849* (BRY). **Idaho**. Bannock Co.: McCammon side of Indian Rocks State Park, dry rocks, with cheatgrass, sagebrush, bitterbrush, and cactus, 4684 ft, 2 Jul 1996 *Chipman 246* (IDS image!, SRP image!), 13 Jul 1996, *Chipman 281* (IDS image!, SRP image!, UTC image!), 6 Aug 1996, *McDougall & Chipman 348* (IDS image!, SRP image!, UTC image!); head of Mill Creek Canyon ca. 4 mi SE of Bancroft, seep area, 6750 ft, 8 Aug 1978, *Foster 7134* (RM). Blaine Co.: Craters of the Moon Natl Reserve, W edge of the Carey lava flow, ca 2 mi E of Carey, in "Crater Lake" area, a large complex of seasonally ephemeral and longer-lasting water pools, 4780 ft, 1 Aug 2006, *Mancuso et al. 2995* (BRY, CRMO image!). Butte Co.: Craters of the Moon Natl. Monument, Big Cinder Butte Flow, 7 Aug 1936, Collector not specified [Natl Park Service] *123* (CIC); Craters of the Moon Natl. Monument, young pahoehoe flow, 5600 ft, 7 Aug 1936, *Eggler 125* (MIN image!). Cassia Co.: Emery Canyon, Silent City of the Rocks, rocky ground, 23 Aug 1951, *Baker 8676* (BRY, ID-2 sheets! images!, NY-4 sheets, UC, WTU-3 sheets); City of Rocks, base of rock, 6000 ft, 17 Jul 1974, *Brown 862* (SRP image!); Keg Hollow Canyon, woodland to rockland, with *Pinus monophylla*, *Juniperus osteospermum*, and *Cercocarpos ledifolius*, 6600 ft, 22 Jul 1974, *Brown 906* (CIC image!, IDS image!); Albion Mts, near City of Rocks, SW of Malta, pinyon-mountain mahogany community, coarse granitic sand, 1 Sep 1982, *Goodrich et al. 17878* (BRY, ID! image!, NY); Albion Mountains, base of granite rocks and in soil pockets on rock faces at Twin Sisters, 10 Jul 1992, *John 796* (IDS image!); City of Rocks, pinyon-juniper, 5700 ft, 16 Sep 1973, *Johnson s.n.* (ID! image!); main climbing area of lower City of Rocks, aspen understory, 6200 ft, 23 Oct 2006, *Mansfield 6231* (CIC image!, ID! image!, NY); Albion Mountains, Sawtooth Natl Forest, Mt. Harrison proposed RNA, just S (below) Peak 8806, ca 1 mi NE of lookout on Mt. Harrison, ca 8 mi SE of Albion, deep, stony soil (quartzite), colluvial, unstable disturbed areas within *Artemisia tridentata* subsp. *vaseyana-Symphoricarpos oreophilus-Bromus carinatus* community, 8700 ft, 10 Aug 1987, *Moseley 1165* (ID! image!); ca 1.5 mi NE of Mount Harrison, *Pinus flexilus*/ *Cercocarpus ledifolius*, 8860 ft, 14 Sep 1973, *Steele 765* (CIC image!, ID! image!); City of Rocks, 28 Jul 1952, *Zappettini 46* (ID! image!). Power Co.: Craters of the Moon Natl Monument, Wapi Park, W end of park by aspen, burned area and adjacent lava flow, 5082 ft, 5 Jul 2002, *Atwood 28744* (CRMO image!, NY); Craters of the Moon Natl Monument, S edge of Wapi Lava Field, 0.2 mi W of Wapi

water tower, transitional edge of Snake River plain, sandy site and fissured Pahoehoe lava flow, 4450 ft, 23 Jun 2006, *Atwood 31595* (CRMO image!); Minadoka Natl Forest, Sublett Division [now Sawtooth NF; the Sublett Division is in SW Power Co.], 6500 ft, 10 Aug 1936, *Richardson s.n.* (ID! image!); Sublett Division, Minadoka Natl Forest [now Sawtooth NF], 6500 ft, 20 Aug 1936, *Richardson 94* (ID! image!). **Nevada**. Clark Co.: Charleston Mts, sandstone cliffs near La Madre Spring [Red Rock Canyon Natl Conservation Area], 4700 ft, 12 Sep 1928, *Jaeger s.n.* (UC); Lincoln City, Condor Canyon, upland community, 5000 ft, 11 May 1988, *Koniak & Nelson s.n.* (BLM Herbarium, Las Vegas Dist image!); E side of Spring Mtns, Calico Hills, Red Spring area [Red Rock Canyon Natl Conservation Area], rock slope, 3651 ft, 27 Sep 1991, *Pinzl 9868* (NY image, UTC image); Muddy Mts, ca. 1.5 mi W of Logandale, Jurrasic outcrop, 1400 ft [m?], 9 Aug 1979, *Swearingen 1206* (RSA); Muddy Mts, uncommon in wash which feeds into Colorado Quarry from unnamed valley, ca. 3000 ft, 11 May 1980, *Swearingen 1428* (RSA). Elko Co.: 0.25 mi W of Collar Elbow Basin, pinyon pine, granitic soil, 7000 ft, 9 Aug 1979, *Foster 8378* (BRY, NY, RM); Ruby Mts, mouth of Lamoille Canyon, dry soil in rock crevices, 14 Aug 1941, *Holmgren 1763* (UC, UTC); N slope of Brown Creek Canyon, dry sagebrush slopes, 7500 ft, 28 Aug 1983, *Holmgren 10265* (BRY, CAS, RSA, WTU); Jarbidge Wilderness, head of Cottonwood drainage, ledges, 9500 ft, 17 Aug 1976, *Lewis & Walters 4538* (BRY); Ruby Mts, Lamoille Canyon, dry wash, 7500 ft, 27 Jul 1940, *Munz 16176* (CAS, POM, UC, WTU); N end of Spruce Mtn, just E of Black Forest Mine Bldg complex, rock-lined narrow canyon, by rock outcrop with *Holodiscus*, 8200 ft, *Pinzl 10152* (TEX); Soldier Creek [labeled as from Humboldt Co.], woodland, 8 Jul 1928, *Price 216* (RM); Ruby Mts, Soldier Creek Trail area, E of Nev Hwy 227, cracks in canyon rock faces, 10 Aug 1990, *Semple et al. 9270* (BRY); Bull Run Mts, ridge just E of the Bull Run Reservoir, 7400 ft, on very steep limestone ridges, 24 Aug 1984, *Tiehm 9295* (BRY, CAS, ID! image!, NY, RSA, TEX, WTU); Jarbidge Mts, lower part of Camp Creek on the E side of the range, near the forks, with *Artemisia* in steep rock outcrops, 7000 ft, 2 Aug 1985, *Tiehm 10070* (BRY, CAS, ID! image!, NY, TEX, VDB); Robinson Creek, E side of Ruby Mts, 7000 ft, 5 Aug 1936, *Train 429* (MO); head of Copper Creek Basin, Jarbidge Mts, lava rimrock crevices, 8200-8800 ft, 6 Aug 1937, *Train 662* (DS, NY); Jarbidge River Canyon, 1-3 mi from Jarbidge, 6800 ft, 17 Aug 1937, *Train 783* (UC); W slope of Ruby Mts, Soldier Creek Canyon at Mine, dry granite slope, 6400 ft, 1 Sep 1940, *Train 4650* (NY, UC); Ruby Mts, Lamoille Canyon, Lamoille Canyon Road, roadside, 2353 m, 30 Aug 2013, *Warman 79* (UTC); Ruby Mts, Lamoille Canyon, 1.9 road mi beyond Thomas Creek Campground, gravelly soil, roadside, 8400 ft, 22 Aug 1984, *Williams 84-105* (BRY, CAS, IDS, NY). Esmerelda Co.: Lone Mt area about 14 mi W of Tonopah, Springdale Canyon on the E side, in granite rock outcrops, 30 Jul 1983, *Tiehm 8250* (BRY, CAS, NY, RSA, TEX). Eureka Co.: Monitor Range, N Fork Allison Creek, ca 34 mi from Austin, 7920 ft, 3 Jul 1979, *Goodrich 13172* (BRY, NY); East Pahranagat Range, 3.7 road mi W of Pahranagat High School in Alamo, on silicic ash flow tuff rock outcrops, 4200 ft, 18 Jun 1982, *Tiehm 7231* (MO); Roberts Creek Mts, Roberts Creek near the campground, in steep limestone outcrops, 7000 ft, 18 Jul 1983, *Tiehm 8179* (CAS, NY, RSA, VDB); Diamond Mts, Davis Canyon on the NW side of the range, 0.2 mi E of the first creek crossing, 7000 ft, in steep rock outcrops N of the road, 19 Jul 1983, *Tiehm 8187* (BRY, CAS, NY, RSA, TEX, WTU); Fish Creek Range, near the entrance to Goodwin Canyon just S of Eureka, in steep limestone outcrop, 6350 ft, 15 Sep 1983, *Tiehm 8414* (CAS, NY, RSA, TEX, VDB); New York Canyon, dry rocky slopes, 7000 ft, 18 Oct 1937, *Train 1248* (DS, MO, UC). Humboldt Co.: Little Humboldt Ranch, 6500 ft, 28 Aug 1940, *Holmgren 756* (BRY, RM, WTU). Lander Co.: 17 mi from Austin, Birch Creek Canyon, dry rocky soil of decomposed granite, 7 Sep 1937, *Henning 41* (NY, UT). Lincoln Co.: Panaca, 5 Sep 1912, *Jones s.n.* (POM-2 sheets); Mt. Irish, Aug 1898, *Purpus 6352* (UC); East Pahranagat Range, 3.7 road mi W of Pahranagat High School in Alamo, tuff rock outcrops, 4200 ft, 15 May 1982, *Tiehm 6890* (CAS) and 18 Jun 1982, *Tiehm 7231* (CAS, NY, RSA); Mahogany Mts, jct of road to Deer Lodge Canyon and the road to Prohibition Flat, in sandstone outcrops near the junction, 6300 ft, 13 Sep 1983, *Tiehm 8375* (CAS, NY, RSA, TEX, VDB); Clover Mts, Pine Canyon Reservoir, just N of the dam, on the W side of the reservoir, with pinyon-juniper, *Artemisia tridentata* on rocky steep slopes, 5740 ft, 5 Sep 2005, *Tiehm 15068* (BRIT, BRY, CAS, ID! image!, NY, RSA); 10 mi W of Crystal Springs, E side Irish Mtn, W side of Pahranagat Valley, 5500 ft, 28 Aug 1938, *Train 2395* (DS, MO, NY); 4 mi N of Caliente on road to Panaca, 4000 ft, 7 Sep 1938, *Train 2473* (UC). Nye Co.: NE Forty-Mile drainage basin, Nevada Test Site, common on cliffs

Figure 11. *Heterotheca cinerascens*, Lincoln Co., Nevada.

Figure 12. *Heterotheca cinerascens*, Eureka Co., Nevada.

Figure 13. *Heterotheca cinerascens*, Elko Co., Nevada.

Figure 14. *Heterotheca cinerascens*, Lander Co., Nevada. *Henning 41* (UTC).

and along rock outcrops of canyon wash, steep-walled canyon N of Twin Peaks, W of Back Rainier Mesa Rd and E of Pahute Mesa Rd, rays deep orange-yellow, 17 Sep 1971, *Beatley 13226* (CAS, NY, RSA, TEX); Nevada Test Site and vicinity, *Beatley 2916*, *3132*, *3930*, *6439*, *6525*, *6582*, *7280, 9693, 9915* (CAS, DS, NY, RSA); S end of Toquima Range NNW of Baxter Spring, canyon bottom, 7200-7600 ft, 25 Aug 1978, *Genz 8895* (BRY); Monitor Range, E Dobbin drainage, Miniature Grand Canyon, crevices, 7500 ft, 26 Sep 1977, *Goodrich 10775* (BRY); Toiyabe Range above Timblin Creek, 35 air mi SE of Austin, cracks and talus, 10,500 ft, 30 Aug 1978, *Goodrich 12236* (BRY, NY); Grant Range, Troy Canyon on W side of the range, 2.2 road mi E of the Nyala road, granite outcrops, 6000 ft, 17 Aug 1983, *Tiehm 8300* (BRY, CAS, NY, RSA, WTU); Monitor Range, East Dobin Creek, Miniature Grand Canyon at the canyon entrance, steep rock outcrops, 7650 ft, 30 Aug 2001, *Tiehm 13761* (BRY, CAS, ID! image!, NY, RSA, UC, WTU). Pershing Co.: Juniper Range, rocks, 6000-7000 ft, May-Oct 1898, *Purpus 6247* (UC); Juniper Mts, 6000-7000 ft, May-Oct 1898, *Purpus 6248* (UC). White Pine Co.: Rocks on W side of cirque on N side of Mt. Sherman, 10,000 ft, 4 Aug 1939, *Hitchcock & Martin 5679* (CAS, DS, IDS image!, NY, RSA, UC, WTU); Cherry Creek, 17 Jul 1891, *Jones s.n.* (POM); [Snake Range], Jeff Davis Mtn, on slopes, 2400 m, 27 Aug 1919, *Tidestrom 11133* (LL); Snake Range, Murphy's Wash at the S end of the range, 4.9 road mi N of Big Springs Wash road, cracks of steep limestone canyon walls, 6600 ft, 9 Aug 1985, *Tiehm 10104* (BRY, CAS, NY, TEX, VDB); Schell Creek Range, McCoy Creek on E side of range, 2 road mi W of main Spring Valley road, rock outcrops, 7000 ft, 10 Aug 1985, *Tiehm 10127* (BRY, CAS, NY); Egan Range, foothills on E side of Jakes Wash, steep sandstone outcrops 6375 ft, 19 Jul 2000, *Tiehm 13328* (BRY, CAS, CIC image!, ID! image!, RSA, UC, WTU); Diamond Mts, Mining Canyon, SE end of range, 11.2 road mi N of Hwy 50 on Rte 892, limestone canyon with pinyon-juniper, 6350 ft, 30 Aug 2009, *Tiehm 15949* (BRY, CAS, CIC image!, NY). **Utah**. Beaver Co.: WahWah Mts, WahWah Mines, 13 air mi S of Wah Wah Pass, among quartzite boulders on N side of canyon, 7800 ft, with ponderosa pine, juniper, and *Cercocarpus*, 8 Aug 1969, *Holmgren 3830* (NY, RSA, WTU); Tushar Mts, Beaver River Canyon, S-facing cliff base, pinyon-juniper-oak-*Cercocarpus*, ca. 7600 ft, 16 Aug 1984, *Taye 3132* (BRY); ca. 5 km E of Beaver on Utah Hwy 153, at boundary of Fish Lake Natl Forest, near creek, edge of Gambel's oak woodland and near volcanic rocks, ca. 6000 ft, 10 Sep 1985, *Semple & Heard 7818* (BRIT, BRY, MO); Wah Wah Mts, Pine Grove Canyon, pinon-juniper woodland, 13 Sep 1963, *Welsh & Christensen 2705* (BRY, NY). Boxelder Co.: Raft River Mts, SW of Strevell, Clear Creek Campground, sagebrush hillside, 6400 ft, 26 Jul 1965, *Erdman 2400* (BRY); Sulphur Springs, Bear River Bay [Great Salt Lake], cliffs in foothills, 14 Aug 1929, *Garrett 5408* (LL) and *Garrett 5408a* (BRY, LL, RM). Iron Co.: Wah Wah Mts, 8 air mi N of Lund, Broae Hill, tuffaceous knoll NE of road across Blawn Wash, ca. 1750 m, 7 Sep 1988, *Ertter 7941* (BRY, NY, RSA, UC); Cedar Breaks, dry meadow, 10,000 ft, 17 Jul 1930, *Goodman & Hitchcock 1618* (DS); Three Peaks Recreational Area, ca 9 mi W to NW of Cedar City, granitic boulders on mountain summit, 1767 m, 24 Sep 2007, *Spujt 16133* (BRIT, RSA); Pine Valley Mts, Paradise Spring Trail, pinyon-juniper-mahogany-oak, 7100 ft, 26 Jun 1986, *Warrick 2182* (BRY). Juab Co.: 8 mi E of Leamington, Dog Valley Wash, ca. 5000 ft, 12 Oct 1983, *Baird 293* (BRY); ca. 15 mi E of Leamington, 8 Sep 1965, *Welsh & Moore 5146* (BRY, NY). Kane Co.: Paria Plateau, 18 Aug 1972, *Atwood & Moore 4286* (ID); 1 km E of Zion Natl Park on Utah Hwy 9, red sand, junipers, 12 Sep 1985, *Semple & Heard 7876* (BRY). Millard Co.: Canyon Mts, Oak Creek near Oak Creek Campground and Guard Station, 4.2 mi SE of Oak City, quartzite outcrop, 6300 ft, 7 Aug 1981, *Goodrich 16084* (BRY); House Range, Painter Spring, granite, riparian, 6500 ft, 2 Sep 1981, *Kass & Preston 624* (BRY); Pavant Range, Piute ATV trail on conglomerate outcrop, white fir community, 7800 ft, 18 Sep 1999, *Tilley 961* (BRY). Piute Co.: Falls of Bullion Creek, [the MO label says "Marysvale, Tate Mine"], 9500 ft, 24 Aug 1894, *Jones 5903* (MO, NY, POM, RM, UC); Bullion Canyon, in and near the Gorge, 27 Jul 1905, *Rydberg & Carlton 7288* (NY, RM-2); Tushar Mts, Bullion Canyon, outcrop cracks, aspen-white fir, 8791 ft, 20 Jul 1990, *Taye 4886* (BRY). San Pete Co.: Maple Canyon, vicinity of Ephraim, 24 Jul 1934, *Olsen s.n.* (UTC image!). Tooele Co.: Sheeprock Mts, narrows of Joe's Canyon, granite outcrop cracks, mountain brush community, 2250 m, 13 Sep 1995, *Bates 918* (BRY); Stansbury Mts, Muskrat Canyon, quartzite slope, 7200 ft, 28 Jul 1981, *Taye 1429* (BRY). Washington Co.: St. George, arid hills near Sugar Loaf, 20 Jun 1942, *Degener & Peiler 16,639* (MO, NY); N of St. George, red sandstone ledges, 3000 ft, 8 Sep 1935, *Galway s.n.* (BRY-2 sheets); 2.8 mi N of St. George on road to Enterprise, dry rocky wash with *Rhus trilobata*, *Juniperus*, and *Artemisia tridentata*, 3000 ft, 7 Sep 1941, *Gould 1357* (CAS, DS, ID!

image!, NY, PH, POM); Dixie State Park, ca. 5 mi NW of Ivins, sandy soil, 3200 ft, 13 May 1967, *Higgins 988* (BRY); Red Mts, Navajo sandstone and blow sand, *Artemisia-Quercus*-mixed shrub, 1250 m, 9 Jun 1999, *Higgins et al. 20387* (RM); Pine Park, conglomerate ash of volcanic origin, ponderosa pine-oak-pinyon-juniper, 1750 m, 25 Sep 1999, *Higgins 20871* (BRY, MO, RM); Zion NP, near canyon bottom, dry hot slopes, 15 Aug 1932, *McDonald 1161* (RM); Zion Natl Park, Narrows Trail, ca. 1 mi N of Temple of Sinawave, 12 Jun 1970, *Moor 2118* (BRY); St. George, 1875, *Palmer s.n.* (MO); W of Leeds on Silver Reef Road, 2.0 km into Dixie Natl Forest, road cut through red sandstone, 10 Aug 1985, *Semple & Heard 7857* (BRY). Wayne Co.: Top of North Caineville Mesa, ca. 16 mi W of Hanksville, cap of Emery sandstone along NW rim, 5900 ft, 6 Sep 1985, *Tuhy 2506* (BRY).

Variant: Leaves widely spaced, oblanceolate, 7 mm wide, 3–4.5 cm long: **Arizona**. Mohave Co.: Short Creek, crevices of rocks, 4500 ft, 10 Jun 1941, *Cottam 8578* (RSA).

Variant: Vestiture completely glabrous, outer phyllaries foliaceous, and heads few-flowered (disc): **Nevada**. Clark Co.: Muddy Mts, 11 May 1980, *Swearingen 1428* (RSA). *Swearingen 1206* (RSA) from the same area is typical *Heterotheca cinerascens*. The Muddy Mountain plants occur at ca. 3000 ft, at the lowermost elevational limit for the species.

Variant: Habit and aspect of *Heterotheca cinerascens* but phyllaries strigose: **Utah**. Washington Co.: Zion Natl Park, Emerald Pool Trail, 9 Oct 1937, *Ramsey 1267* (POM) and *Ramsey 1268* (POM).

Variant: Some collections from Zion National Park resemble *Heterotheca cinerascens* in vestiture but have long (40–50 cm), lax-flexuous stems, thin leaves relatively evenly spaced and even-sized (all the way to the heads), and solitary heads (on long peduncles). These are consistent in aspect and apparently are plants with suppressed lateral buds (buds sometimes occur in nodes immediately below the heads). **Utah**. Washington Co.: The Narrows Trail, 8 Sep 1938, *Eastwood & Howell 6325* (CAS); The Narrows Trail, 13 Sep 1968, *Howell & True 45301* (CAS); Zion Natl Park, no other locality data, 25 Jun 1933, *Eastwood & Howell 1105-a* (CAS); Zion Natl Park, Narrows Trail, rocky slopes, ca. 4420 ft, 30 Sep 1972, *Nelson 10134* (RM); Zion Natl Park, no other locality data, 24 Sep 1928, *Thackery 507* (TEX-2 sheets); Zion Natl Park, Zion Canyon, N Fork Virgin River, along river bottom, between trailhead and The Narrows, riparian, on alluvium, 8 Aug 1987, *Thorne & Chandler 5586* (RM); Zion Natl Park, side canyon of Clear Creek along Washington-Kane county line, Navajo sandstone, 5240 ft, 15 Oct 1987, *Thorne & Franklin 5749* (RM). This distinctive growth form, with solitary heads on long, flexuous stems, also occurs in plants identified here as *H. zionensis*, e.g., **Utah**. Garfield Co.: California Creek Canyon, *Cox & Baumann s.n.* (BRY). Washington Co.: South Ash Creek, *Warrick 2717* (BRY). On the other hand, typical plants of *H. cinerascens* occur in the same area of Zion National Park (see citations above) and these monocephalous variants, highly distinctive in appearance, should be studied further.

4. HETEROTHECA JOSHUANA Nesom, **sp. nov. TYPE**: **California**. San Bernadino Co.: Joshua Tree Natl Park, Little San Bernardino Mts, Queen Mountain, near Oak Canyon, bouldery wash, locally infrequent in boulder crevices, 1460 m, 3 Nov 2008, *T. LaDoux et al. 1841* (holotype: JOTR image!, Fig. 15).

Similar to *Heterotheca cinerascens* in aspects of vestiture (especially leaves with glandular surfaces and phyllaries glandular and without other hairs), different in its (1) stems with fine, spreading-ascending hairs (vs. puberulent-hirsutulous with patent hairs), (2) leaves linear to linear-lanceolate, sharp-pointed and apiculate, even-sized, and densely arranged (vs. narrowly elliptic-oblanceolate to elliptic, apex rounded, usually diminishing in size distally, characteristically more widely spaced), (3) heads smaller (rays 6–14 vs 10–17, involucres (5–)6–9 mm wide vs (7–)9–11 mm wide), and (4) consistent lack of prominent capitular bracts.

Plants perennial from a woody taproot; axillary buds produced along entire length of the stems. **Stems** mostly 20–25 cm, erect or slightly ascending from the base, internodes 1–7 mm long, densely minutely glandular, sparsely hirsute-strigose to stiffly villosulous with fine, spreading to spreading-ascending or ascending hairs of relatively even length. **Leaves**: basal and lowermost spatulate with narrow petiole, mostly 15–23 mm, cauline abruptly linear to linear-lanceolate, linear-oblanceolate, or narrowly elliptic-lanceolate, 5–17(–21) x 1–2.5(–)4 mm, distally carinate, epetiolate, stiffly spreading, continuing mostly unreduced in size up to the heads, apex sharply acute with a long, white-indurate, sharp-pointed, straight to slightly falcate apiculum, both surfaces minutely glandular, hirsute with ascending hairs to hispid-hirsute, margins eciliate. **Heads** solitary or 2–8 in a loosely corymboid cluster, peduncles 10–20 mm, capitular bracts linear to linear-lanceolate and very small if present, usually not evident; involucres (5–)6–9 mm wide, inner phyllaries 6–7 mm long, narrowly oblong-lanceolate, slightly keeled, sessile-glandular to minutely stipitate-glandular, without other hairs. **Ray flowers** 6–14, laminae ca. 1 mm wide. Chromosome number unknown.

Flowering (Apr–)Aug–Nov. Rocky habitats, commonly with *Quercus cornelius-mulleri*, *Pinus monophylla*, *Nolina parryi*, *Acacia greggii*, *Haplopappus cuneatus*, *Opuntia phaeacantha*, and *Opuntia basilaris*; ca. 2400–5200 ft (–5500 ft at top of Queen Mtn in Joshua Tree Natl Park). Little San Bernadino Mountains of Riverside and San Bernadino counties, California.

Heterotheca joshuana is distinctive in its linear to linear-lanceolate, even-sized, and densely arranged leaves (short internodes) with a long, white-indurate, sharp-pointed, straight to slightly falcate apiculum. Identification is further secure as *H. joshuana* apparently does not occur in sympatry with any other *Heterotheca* species and no similar species occurs in California, Arizona, or Mexico. Obvious similarities in vestiture and leaf arrangement and geographical proximity suggest that it is closely related to more northern *H. cinerascens* but the California plants are about 200 miles disjunct from the nearest populations of *H. cinerascens* in Clark and Nye cos., Nevada. While most of the Nevada and Idaho population systems of *H. cinerascens* also are essentially isolated and geographically disjunct from one another, the *H. joshuana* system is more distantly isolated and in a different ecology — the Colorado Desert (part of the Sonoran Desert) and Mojave Desert, both of which occur in the Joshua Tree National Park. It is a reasonable hypothesis that *H. joshuana* and *H. cinerascens* are sister taxa, with *H. joshuana* more derived in morphology than the widespread *H. cinerascens*.

Additional collections. California. Riverside Co.: Joshua Tree Natl Monument, Barker Dam, 4300 ft, 14 Oct 1966, *Baker & Baker s.n.* (JOTR image!); Joshua Tree Natl Monument, 1/2 mi S of Desert Queen Mine, boulder crevice, 4400 ft, 19 Oct 1966, *Baker & Baker s.n.* (JOTR image!); Joshua Tree Natl Monument at campground area by Hidden Valley, 9 Oct 1947, *Dunn 3533* (MO); Little San Bernadino Mts [W end], Morongo Pass [ca. 7 mi N of Whitewater on Hwy 62, at ca. 2400 ft], 15 Nov 1921, *Jaeger s.n.* ([POM]); Joshua Tree Natl Park, Little San Bernardino Mountains, Wonderland Wash, N of Wall Street Mill parking area, frequent on bouldery outcrops above wash, 4319 ft, 17 Aug 2005, *LaDoux 1545* (JOTR image!); Keyes Ranch, Morongo Pass, among rocks, 4000 ft, 30 Apr 1921, *Munz 4536* ([POM]); Wonderland of Rocks, Joshua Tree Natl Monument, 24 Oct 1942, *Roos 2571* ([POM]); Little San Bernadino Mts, [Joshua Tree Natl Park], Wonderland of Rocks, crevices in boulders, 4000 ft, 21 Oct 1950, *Roos 5011* (DS, NY, [RSA], UCR); Joshua Tree Natl Monument, granitic rocks at Hidden Valley Campground, 22 Aug 1979, *Thorne 53595* ([RSA]). San Bernadino Co.: Joshua Tree Natl Park, top of Queen Mountain, along climber's trail just W of peak, rocky wash and surrounding large bedrock outcrops, frequent through rock outcrops, 5182 ft, 5 Oct 2011, *Harding 31* (JOTR image!); Joshua Tree Natl Park, Queen Valley, Wonderland of Rocks near Wonderland Wash, 18 Sep 2012, *LaDoux et al. 3141* (JOTR image!). Colllections cited by the Consortium of California Herbaria at POM-RSA were unavailable for study when I was there in 2016.

Figure 15. *Heterotheca joshuana*, holotype.

5. HETEROTHECA SHEVOCKII (Semple) Semple, Univ. Waterloo Biol. Ser. 37 (Rev. Heterotheca Phyllotheca): 148. 1996. *Heterotheca villosa* var. *shevockii* Semple, Phytologia 73: 453. 1992 [published 1993]. **TYPE**: **California**. Kern Co.: S end of Hot Springs Valley between Bodfish and Lake Isabella, at onramp of California Hwy 117 adjacent to Kern River, granitic roadbank of hwy with *Eriogonum fasciculatum* and ruderal vegetation, 2465 ft, 16 Nov 1981, *J. Shevock 9110* (holotype: CAS image!; isotype: WAT).

Heterotheca shevockii grows only along the Kern River below Lake Isabella in chaparral and woodland habitat in sandy soils in crevices and ditches near the river and along roadsides. It has been abundantly collected. Apparently no other species of *Heterotheca* occurs in the same area. In its original description (as "var. *shevockii*"), Semple noted that it is "distinguished from other races of [*Heterotheca villosa*] by its unusually tall stems [up to 2 meters, pers. observ.] and lanceolate-deltoid leaves with inrolled margins. Smaller plants are similar to [*H. polothrix*] to which [*H. shevockii*] is undoubtedly closely related." The heads are large and without capitular bracts. Given its distinctive morphology and geography, it is securely identified but its evolutionary affinity is uncertain.

6. HETEROTHECA HIRSUTA (Greene) Nesom, **comb. nov.** *Chrysopsis hirsuta* Greene, Pittonia 3: 296. 1898. **TYPE**: **Washington**. [Spokane Co.]: Near Spokane, banks of Hangman Creek, 3 Sep 1896, *C.V. Piper 2385* (holotype: NDG 53918, Fig 17; isotype: GH image!).

Chrysopsis barbata Rydb., Bull. Torrey Bot. Club 37: 130. 1910. *Heterotheca barbata* (Rydb.) Semple, Brittonia 39: 379. 1987. **TYPE: USA. Idaho**. Kootenai Co.: Valley of Spokane River, 17 Jul 1893, *J.H. Sandberg, D.T. MacDougal, & A.A. Heller 664* (holotype: NY image!; isotypes: CAS! image!, GH-Fig. 18!, US image!).

Semple (1996) placed *Chrysopsis hirsuta* as a synonym of *Heterotheca villosa* var. *minor* but the type of *C. hirsuta* is essentially identical in morphology to the *C. barbata* type and probably was collected no more than 30 miles from the *C. barbata* type locality. Kootenai Co. (Idaho) and Spokane Co. (Washington) are directly adjacent on opposite sides of the Spokane River.

Chrysopsis elata Osterh., Bull. Torrey Bot. Club 57: 560. 1931. **TYPE**: **Colorado**. Eagle Co.: Red Cliff, 16 Aug 1906, *G.F. Osterhout 3359* (holotype: RM image!; isotype: NY image!).

The protologue states that Osterhout "3335" is the type, but the RM and NY sheets both are labeled with the collection number "3359." The original manuscript, in Osterhout's hand, is stapled to the RM holotype and has "3359" as the type number. On Osterhout's distinctive red-colored type label, C.L. Porter in 1950 noted that publication of the number "3335"was in error.

Chrysopsis resinolens var. *ciliata* A. Nels., Bull. Torrey Bot. Club 28: 233. 1901. *Chrysopsis viscida* var. *ciliata* (A. Nels.) Blake in Tidestrom, Contr. U.S. Natl. Herb. 25: 537. 1925. **TYPE**: **USA**. **Wyoming**. Albany Co.: Dunn's Ranch, sandy river bottoms, 16 Jul 1900, *A. Nelson 7566* (holotype: RM! image!; isotype: NY image!, Fig. 22).

The collection number cited in the protologue is "Nelson 7560" and the NY specimen is labeled as "7560 ... n. var." on a label (ex Rocky Mountain Herbarium) apparently handwritten by Nelson, with "Dunns Ranch, July 16, 1900." The RM specimen, however, is labeled 7566 and Nelson's original notes state that 7566 = *Chrysopsis resinolens* var. *ciliata*; Nelson 7560 is listed as a moss (*Mnium serratum*). Thus the collection number in the protologue as well as the label on the NY collection are interpreted as resulting from errors in transcription, and holotype and isotype appear secure as cited here. The RM and NY collections are clearly the same entity.

Stems 15–40 cm, sparsely to moderately hirsute to hirsute-villous or villous with spreading to slightly deflexed hairs, sparsely to densely minutely glandular. **Leaves** cauline, narrowly elliptic to elliptic-lanceolate or elliptic-oblanceolate, essentially epetiolate, mostly 2–4.5 cm, largest at midstem, leaf and bract surfaces loosely strigose to hirsute or hirsute-villous, at least the distal evidently sessile-glandular, petiole margins and at least proximal blade margins evenly long-ciliate. **Heads** more or less

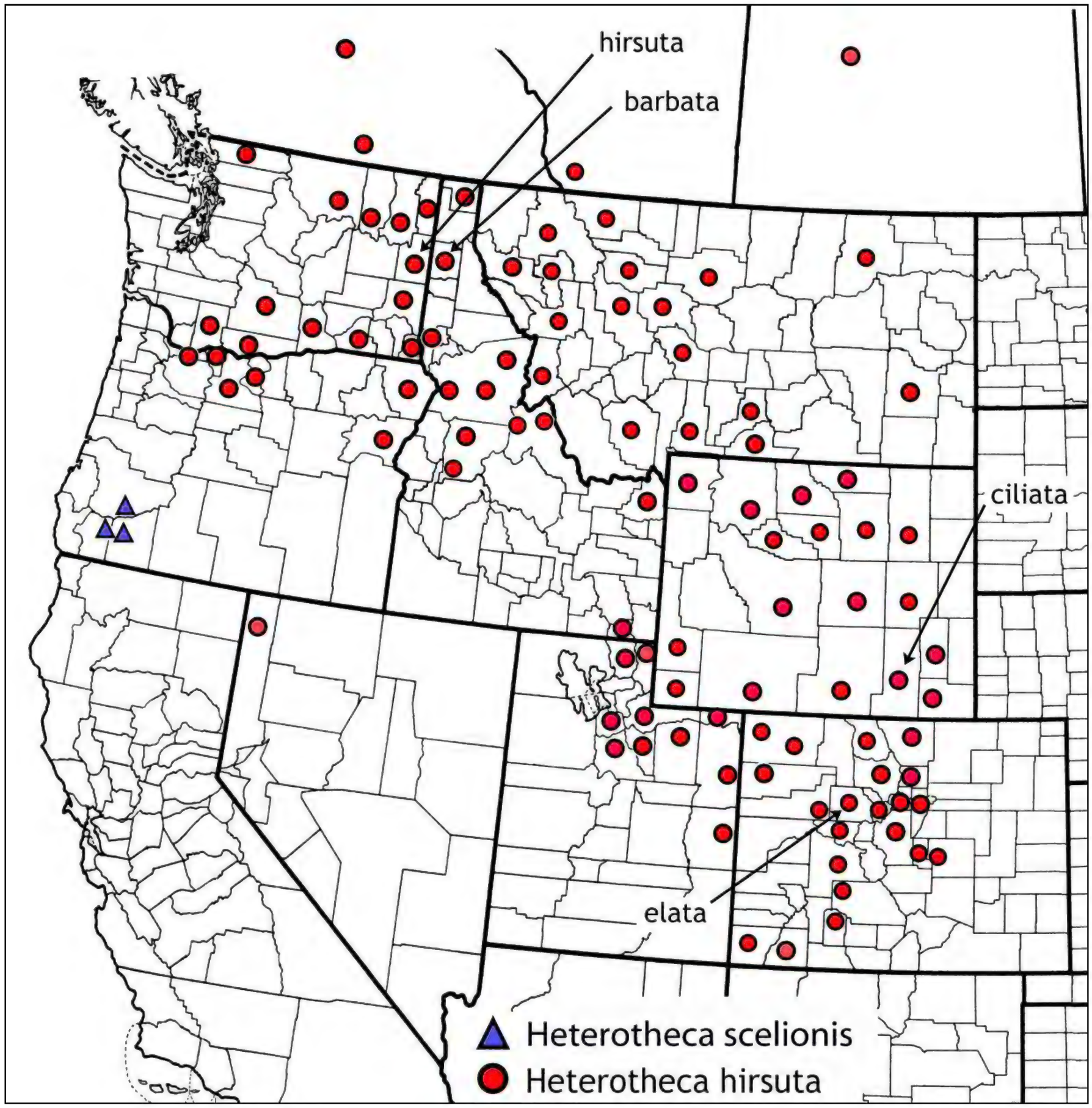


Figure 16. Distribution of *Heterotheca hirsuta* and *H. scelionis*. Arrows point to localities for the type and synonyms of *H. hirsuta*.

solitary on leafy-bracteate peduncles 4–10(–15) cm long, sometimes loosely corymboid; capitular bracts linear-oblong to linear-oblanceolate or oblanceolate, sometimes longer than the phyllaries. **Involucres** 8–12 mm wide; phyllaries 8–10 mm long, narrowly lanceolate to linear-lanceolate, sparsely villous, eglandular or minutely glandular distally. Chromosome number, 2*n*=18 (*Semple 9247* from Salt Lake Co., Utah; *Windham 97-133* from Cache Co., Utah).

Aven Nelson described this taxon as a variety of *Heterotheca* [Chrysopsis] *resinolens*, but it is not clear that *H. resinolens* (in the sense of the present study) is closely related. The two are similar in their prominent capitular bracts and conspicuous sessile glands and relatively reduced non-glandular vestiture (the plants often with a dark green color), but *H. resinolens* differs in its larger stature, larger and more closely spaced leaves, larger heads with broader capitular bracts, and lack of coarsely ciliate leaves and bracts. It has a different geographical range and generally grows at higher elevations.

Figure 17. *Heterotheca hirsuta*. Spokane Co., Washington. Holotype of *Chrysopsis hirsuta*.

Figure 18. *Heterotheca hirsuta*. Kootenai Co., Idaho. Isotype of *Chrysopsis barbata*.

Figure 19. *Heterotheca hirsuta*, Lehmi Co., Idaho. *Romano 269* (SRP).

Figure 20. *Heterotheca hirsuta*. Albany Co., Wyoming. Isotype of *Chrysopsis resinolens var. ciliata*.

Figure 21. *Heterotheca hirsuta*, Natrona Co., Wyoming. *Hartman 38145* (RM).

Figure 22. *Heterotheca hirsuta*, Washoe Co., Nevada. *Tiehm 10816* (NY).

I first identified and annotated *Heterotheca hirsuta* and "*Heterotheca* [Chrysopsis] *elata*" (or "*Heterotheca ciliata*") as separate species, concluding only later in the study, especially when looking at numerous collections from Idaho and western Montana, that a geographic discontinuity in their morphology was not easily apparent. Over the whole range, the plants have relatively sparse (though variable) leaf and stem vestiture of non-glandular hairs but leaf and bract surfaces usually are prominently sessile-glandular. Leaves (including petioles) and bracts are coarsely ciliate at least on the proximal margins. Capitular bracts are consistent and characteristic.

In Oregon, Washington, and Idaho (compared to Montana, Wyoming, Utah, and Colorado), leaf and bract margins of *Heterotheca hirsuta* often are evenly long-ciliate along the whole length, matching the long-hirsute stems and commonly giving the whole plant a shaggy appearance, stems are relatively taller and usually more strictly erect, axillary branches are longer, leaves are longer and narrower, and phyllaries are narrower. *Heterotheca hirsuta* in this area may prove to be evolutionarily distinct, and given the variability within the species as identified here and its wide range, it would not be surprising to find that more than a single entity is represented.

Some morphological variants of *Heterotheca hirsuta* in Montana and Wyoming perhaps reflect influence of sympatric *H. hispida*, which in typical form can hardly be confused with *H. hirsuta*.

Although the range of typical *Heterotheca hirsuta* reaches into central and southwestern Colorado, it has not been commonly collected there. The plants apparently long-disjunct in Washoe Co., Nevada (Fig. 22), are typical of the southern plants.

Additional (representative) collections examined. **CANADA**. **Alberta**. Lee Creek near golf course, Cardston, riverbottom forest, gravelly soil, 3800 ft, 24 Jul 1972, *Shaw 1681* (BRY). **British Columbia**. 1 mi N of Heffley along road to Little Fork, N. Thompson River, open wooded slopes, 1400 ft, 15 Jun 1956, *Calder et al. 17499* (UC); 5 mi E of Grand Forks, dry N slope of valley, roadside, 31 Aug 1937, *McCabe 4640* (UC). **Saskatchewan**. Nisbet Provincial Forest, a few mi E of Prince Albert, sandy jack pine woods, 20 Jun 1949, *Boivin & Breitung 6107* (NY). **USA**. **Colorado**. Boulder Co.: El Dorado Springs State Park, South Boulder Creek at emergence from the canyon, ca. 5500-6000 ft, 30 Aug 1981, *Brewster 47* (BRY); railroad ROW, E of Tunnel 10, near El Dorado Spgs, 22 Aug 1964, *Evers 81308* (MO); Hwy 119 in Clear Creek Canyon, 2408 m, 20 Oct 1998, *King & Garvey 10804* (MO); SW of Lyons, S. Drain River, 6500 ft, 28 Jun 1939, *Rose 39355* (CAS); Comforter Mtn, Boulder Creek Canyon, *Pinus ponderosa*, 7000 ft, 17 Jul 1979, *Taylor 7196* (TEX); Rogers Park, Boulder Canyon, ca 3 mi above Boulder Falls, canyonsides and gravelly flats, 6 Aug 1953, *Weber 8627* (CAS); ca. 7 mi W of Boulder, Boulder Canyon just above Boulder Falls, base of cliffs on S-facing slope, ca. 7000 ft, 2 Oct 1970, *Weber 14419* (NY); along State Hwy 7, St. Vrain River, ca. 0.5 mi SW of mouth of Deadman Gulch and 4.5 mi SW of Lyons, 5720 ft, ponderosa pine, 17 Sep 1984, *Wilken 14298* (BRY, NY). Clear Creek Co.: rocky precipes of Georgetown Pass, 28 Aug 1874, *Engelmann s.n.* (MO); rocks of Georgetown Pass, near Empire, 5 Aug 1874, *Engelmann s.n.* (MO); near Clear Lake, Georgetown, among rocks, 17 Aug 1895, *Shear 4532* (RM). Eagle Co.: Sawatch Range, White River Natl Forest, Homestake Rd, ca. 13 air mi S of Dowds Junction, 6 mi W of US Hwy 24, lodgepole pine, 9160 ft, 12 Aug 2010, *Kirkpatrick 4441* (RM). El Paso Co.: Rainbow Gulch, 800 m W of Rampart Reservoir, 9100 ft, 6 Sep 1989, *Beland & Corkran 47* (RM). Garfield Co.: Flat Tops/White River Plateau, Flat Tops Wilderness, Devils Causeway, ca. 15 air mi SW of Yampa, narrow basal ridge, 11,700 ft, 22 Aug 1991, *Vanderhorst 4294* (RM); Flat Tops/White River Plateau, Main Elk Creek, ca. 15 air mi WNW of Glenwood Spgs, bottom of shale slopes with sagebrush, 5800 ft, 20 Sep 1991, *Vanderhorst 4536* (RM). Gilpin Co.: ca. 4 air mi WNW of Central City, 6.5 air mi NE of Empire along small stream through spruce, 9800 ft, 10 Aug 2003, *Foley 4621* (NY); small lake 1/4 mi below Tolland, prairie, ca. 8800 ft, 19 Aug 1907, *Ramaley & Robbins 3444* (RM); Tolland, 10 Aug 1935, *Zobel s.n.* (MO). Grand Co.: canyon walls just E of Hot Sulphur

Springs at MILE 21 on Hwy 40, 11 Aug 2010, *Atwood 33657* (BRY). Gunnison Co.: West Elk Creek, dry rocky soil, 7460 ft, 11 Jul 1961, *Stock 423* - x *H. paniculata*? (MO). Jackson Co.: summit of North Park Range, rocky ledges, 10 Aug 1903, *Goodding 1826* (RM). Jefferson Co.: Kerr Gulch Rd, ca. 3 mi S of I-70, 2263 m, 15 Aug 1999, *King & Garvey 11105* (BRIT, MO, NY). La Plata Co.: Las Animas [river], Durango, mesa among oaks, 2 Jul 1907, *Clements s.n.* (NY — without capitular bracts but = *H. hirsuta* in all other features). Larimer Co.: Loveland, Thompson Cañon, among rocks, 9000 ft, 5-10 Aug [no year], *Johnston 699* (NY); Hwy 34 just W of Loveland city limits, 23 Aug 1998, *King & Garvey 10700* (MO); Poudre Canyon along Hwy 14, ca 5 mi E of Stove Prairie Rd, ca. 5800 ft, 27 Sep 1998, *King & Garvey 10785* (MO; Big Thompson Canyon on US Hwy 34, ca. 5 mi W of Drake, ca. 1785 m, 20 Aug 1999, *King & Garvey 11120* (BRIT, MO, NY); Cherokee Park, rich meadow, 30 Jul 1923, *Nelson 10007* (MO, RM); Medicine Bow Mts, Laramie River valley from Rawah Trailhead on Laramie River Rd (Co. Rd. 103), ca. 41 air mi NW of Ft. Collins, lodgepole pine, 8300-8500 ft, 20 Jul 2001, *Nunn 3160* (BRY, RM); Dale Creek, 14 Aug 1916, *Osterhout 5521* (RM-2); Dale Creek, 14 Aug 1916, *Osterhout 5522* (BRY); Thompson Canyon, 25 Aug 1916, *Osterhout 5542* (BRY, POM, RM); mts of Estes Park, Windy Gulch, 7 Sep 1916, *Osterhout 5553* (POM). Mineral Co.: Wagon Wheel Gap, 8500 ft, 25 Aug 1912, *Griffin 173 (RM)*. Moffat Co.: Dinosaur Natl. Mon, 1.25 mi S of Lodore Ranger Station, E side of Green River, ca. 1/4 mi SE of Gates of Lodore, pinyon-juniper, 5800 ft, 10 Jun 1987, *Neely 4245* (COLO, RM); Dinosaur Natl. Mon, ca. 1 mi E of Gates of Lodore, pinyon-juniper, 11 Jun 1987, *Neely 4267* (COLO, RM); Yampa River between Craig and Maybell, N side of Duffy Mtn near Sand Spring Gulch, sagebrush scrub, 6100 ft, 15 Aug 1984, *Stein 1901* (MO, RM). [Montezuma Co.: Mesa Verde Natl Park], "sw Colorado, Johnston Cañon," Aug 1892, *Eastwood s.n.* (CAS). Park Co.: Hwy 285 ca. 1/2 mi E of Bailey, 8176 ft, 16 Jul 2003, *King & Garvey 12548* (MO); NW of Lake George, Round Mtn, Campground on US Hwy 24, ponderosa pine, 7 Sep 1985, *Semple 7731* (MO). Pitkin Co.: 7 mi SE of Aspen along State Rte 82, 29 Jun 1981, *Nelson 6554* (RM); Hwy 82, 6.6 km E of Aspen, roadside, broadleaf and conifer, 29 Aug 1995, *Semple 10446* (NY). Rio Blanco Co.: Flat Tops/White River Plateau, Flat Tops Wilderness, Marvine Lakes, ca. 29 air mi ESE of Meeker, rocky area, 9300 ft, 17 Aug 1990, *Vanderhorst 1879* (RM); 1.8 mi WSW of jct of E and W Forks of Fawn Creek, pine and amelanchier, 2215 m, 24 Jun 1982, *Walker & Riefler 82-260* (NY); 4 mi W of Rangely on N side of White River, crevices, white sandstone cuesta, 1600 m, 15 Jun 1978, *Weber 15398* (COLO-2 sheets); ca. 19 mi E of Dinosaur, salt desert shrub community, sandstone outcrops, 5500 ft, 10 Aug 1979, *Welsh 320* (BRY). Saguache Co.: Cochetopa Hills, road to Spanish Creek, ca. 0.5 air mi N of Colo Hwy 114, ca. 20 air mi WNW of Saguache, stream side, rocky slopes, 8700 ft, 3 Jul 1998, *Hartman 61969* (RM). Salt Lake Co.: Wasatch Mts, Big Cottonwood Canyon, 9100 ft, 5 Aug 1905, *Garrett 1585* (PH). Summit Co.: 2 mi E of Frisco on Hwy 9, open area near pine forest, 29 Jul 1978, *Lowry 1303* (NY); town of Frisco, weedy lot, 2770 m, 16 Aug 1991, *Miller et al. 6831* - x pumila? (MO, WTU); Gore Range, Arapaho Natl Forest, S base of Green Mtn along Co. Rd. 30, above Green Mtn Reservoir, ca. 22 air mi NE of Silverthorne at I-70, cliffs, 8000 ft, 16 Aug 2011, *Nelson 83663* (RM). Teller Co.: Manitou Expt Station, 7700 ft, 22 Aug 1963, *Gierisch 2649* (RM); Co. Road 42 in Florissant Fossil Bed Natl Monument, ca. 5 mi SE of Florissant, 8560 ft, 23 Aug 20000, *King & Garvey 11547* (MO; near Florissant, ca. 2400 m, 1-8 Aug 1905, *Ramaley1401* (RM). **Idaho**. Boundary Co.: 1 mi N of Bonners Ferry, sandy hillside, 9 Aug 1955, *Baker 13865* (ID, WTU); just S of Naples, sandy, dune-like soil in *Pseudotsuga* woodland, 1 Aug 1953, *Keck 6541* (UC). Franklin Co.: Franklin Basin, White Canyon, 8300 ft, 30 Jul 1958, *Cottam et al. 15304* (BRY, DS). Fremont Co.: Willow Creek RNA, sandy loam on basalt, 5850 ft, 28 Aug 1985, *Wellner 3586* (ID). Idaho Co.: Salmon River ca. 1 mi S of Slate Creek, dry rocky bank, 4 Aug 1951, *Baker 8368* (ID, WTU-2 sheets); Middle Fork of Clearwater River at mouth of Three Devils Creek, sandy, exposed N bank, 1400 ft, 12 Jul 1937, *Constance 1978* (UC, WTU); mouth of Salmon River, 27 Jun 1925, *Eastwood 13292* (CAS); ca. 1.6 air mi W of Blackhawk Bar on the Salmon River above the Crooked Road (672) on the ridge between Rhett Creek and Christie Creek, rocky ridge, lodgepole pine, 4460 ft, 12 Aug 2004, *Hays 2761* (ID); Middle Fork of the Clearwater River, near Three Devils Creek, sandy bar,

17 Aug 1950, *Jones 363* (DS, NY, RSA, SMU, WTU); Selway Falls, no date, *Rust 2601* (ID); 15 mi N of Riggins, Christie Creek, 23 Jul 1963, *Schlatterer 136* (ID). Kootenai Co.: mountain sides, Jun 1888, *Sandberg s.n.* (BRIT); mountainside, Jun 1890, *Sandberg s.n.* (UC). Lehmi Co.: Challis Natl Forest, Warm Spring Creek drainage, by hotsprings ca. 0.25 mi up Hot Creek, dry outcrops, 5600 ft, 25 Jul 1980, *Brunsfeld 1624* [x *H. vespertina*] (ID); Salmon Natl Forest, near the mouth of Jacks Creek along the Middle Fork Salmon River trail, flat rocky area, 3560 ft, 2 Jun 1992, *Mancuso 651* (ID image!, SRP image!); Salmon Natl Forest, Fenster Creek, 4500 ft, 25 Jun 1929, *Romano 269* (RM, SRP image!). Nez Perces Co.: along Hatwai Creek, dry bank and copses, 17 Jun 1894, *Henderson 2805* [x *H. hispida*] (RM). Valley Co.: 3-4 mi E of Lick Creek Summit along main road, sandy granitic soil along road in mtn brush community, 27 Jul 1988, *Atwood 13419* (BRY, NY, RM, RSA); above Trail Creek Campground, ca. 5000 ft, 9 Jun 2003, *Davis 247* (BRY). **Montana**. Carbon Co.: 40.5 mi NE of Cook City, above head of Wyoming Creek on Line Creek Plateau, 9994 ft, 6 Aug 1988, *Thorne 6544* (BRY). Cascade Co.: Great Falls, 9 Jul 1895, *Anderson 120* (UC); Little Belt Mts, Smith River, mouth of Trout Creek and up Trout Creek ca. 0.5 mi, 31 air mi S of Great Falls, dry creek bed, 1183 m, 15 Jul 2009, *McNeill 6579* (RM). Chouteau Co.: Square Butte, E base, ca. 32 air mi SE of Ft. Benton, rocky slope, pine-fir, 1342 m, 3 Jul 2009, *McNeill 5707* (RM); Turecks Ranch, ESE of Square Butte, ca. 33 air mi SE of Ft. Benton, open meadow, dry draw, 1184 m, 3 Jul 2009, *McNeill 5838* (RM). Custer Co.: Miles City, westernmost exit on I-94, 24 Aug 1975, *Semple 2026* (MO). Flathead Co.: Mt Holbrook, Big Prairie, 4900 ft, 27 Aug 1925, *Kirkwood 2234* (RM); Big Fork, 1000 m, 24 Jul 1901, *MacDougal 755* (NY). Gallatin Co.: Madison Range, Gallatin Natl Forest, along Deer Creek Trail ca. 2-3 mi W of Hwy 191, ca. 27 mi SSW of Bozeman, S-facing talus, 7300 ft, 11 Aug 1990, *Evert 20288* (RM). Glacier Co.: Browning, near S city limits, prairie roadside, 1 Aug 1973, *Harms 20226* (KANU image). Lake Co.: Ravalli, 26 Aug 1908, *Butler 121* (NY); Jocks River near Ravalli, Aug 1897, *Elrod 200* (NY); 2 mi S of Polson, open grassy hills, 27 Jun 1948, *Hitchcock 17751* (ID, RM, WTU). Madison Co.: 5 mi SW of Anceney, dry slope in pasture, 5 Jul 1948, *Booth 2894* (WTU). Lewis & Clark Co.: Lewis & Clark Natl Forest, Sawmill Flats on Forest Rd 233, ca. 3.5 air mi S of Gibson Overlook, open meadow, 1556 m, 30 Jul 2008, *McNeill 2989* (RM). Madison Co.: 5 mi SW of Anceney, pasture, 5 Jul 1948, *Booth 2894* (RM). Meagher Co.: 10 mi NW of White Sulphur Springs, shale outcrop, 8 Jul 1947, *Hitchcock 16178* (ID). Missoula Co.: ca. 10 mi up Blackfoot Canyon above Bonner, rocky embankment, 25 Jul 1945, *Hitchcock & Muhlick 11448* - x *H. hispida*? (MO, NY, RM); Missoula, near campus, 3200 ft, 30 Jun 1921, *Kirkwood 1337* (DS); E of Missoula, Mt. Jumbo, below 300 year tree, 11 Jun 1935, *Rose 234* x *H. hispida*? (ID, MO); just N of Missoula, ridge of Waterworks Hill, dry rocky soil, 3300 ft, 4 Jun 1966, *Woodland 250* (DS). Park Co.: along N side of Yellowstone River just W of Bear Creek, 2 mi E of Gardiner, Gallatin Natl Forest, saltbrush-greasewood grassland, barren S-facing slope, 5300-5400 ft, 29 Jun 1998, *Evert 35208* (RM); Yellowstone Natl Park, NW side of Mt. Everts, just above Rescue Creek Trailhead, 1 mi S of Gardiner, 5500 ft, 1 Jul 1998, *Evert 35478* (RM). Teton Co.: Lewis & Clark Natl Forest, S slope of Elk Hill along FS Trail 268, ca. 7 air mi NW of Mortimer Gulch, open dry meadow, 1596 m, 15 Aug 2008, *McNeill 3704* [x *H. hispida*] (RM); Lewis & Clark Natl Forest, confluence of the N Fork Sun River and Circle Creek, ca. 7 air mi NW of Mortimer Gulch Campground, island and riparian, 1495 m, 15 Aug 2008, *McNeill 3724* (RM); Lewis & Clark Natl Forest, N Fork Sun River valley, along FS Trail 268, from S slope of Elk Hill to jct Trail 201, meadow, 1641 m, 16 Aug 2008, *McNeill 3752* (RM). Sanders Co.: National Bison Range, 1966-1968, *Thomas 11866*, *13205*, *14655*, and *14773* (DS). Valley Co.: Bull Pasture Coulee and above, E of Windy Ridge, ca. 1.5 air mi NE of Erie Reservoir, ca. 17 air mi N of Hinsdale, sandstone outcrop, 2520-2680 ft, 27 Jul 2010, *Charboneau 2348* (RM). **Nevada**. Washoe Co.: Granite Range, steep unnamed canyon on SW end of range, S of Granite Peak, 7000 ft, along a steep canyon of granite rocks, 30 Jul 1986, *Tiehm 10816* (BRY, CAS, COLO, ID, NCSC, NY-Fig. 22, RM, RSA, TEX). **Oregon**. Baker Co.: limestone rocks of Hurricane Creek, 28 Aug 1898, *Cusick 2186* (WTU); rocky slopes of Wallowa Mts near Cornucopia, 18 Jul 1936, *Thompson 13325* (CAS, MO, RSA, WTU). Hood River Co.: Hood River, 10 Aug 1928, *Suksdorf 3399* (ID, x *H. vespertina*); near Cornucopia, rocky slopes

of Wallowa Mts, 18 Jul 1936, *Thompson 13325* (PH). Multnomah Co.: Woodville, Jun 1888, *Howell s.n.* (PH). Sherman Co.: Wallowa Mts, limestone rocks, 9 Aug 1898, *Cusick 2074* (DS, MO, UC); Wallowa Mts, limestone rocks of Hurricane Creek, 28 Aug 1898, *Cusick 2186* (MO, UC); near mouth of John Day, dry sandy hillsides, 25 May 1925, *Henderson 5265* (DS, MO). Wallowa Co.: Wallowa Mts, limestone rocks, 9 Aug 1898, *Cusick 2074* - x *H. hispida*? (MO, RM-2 sheets); Wallowa Mts, limestone rocks of Hurricane Creek, 28 Aug 1898, Cusick 2186 - x *H. hispida*? (MO); 4 mi from Inmaha on road to Joseph, rocky slope, 2 Jul 1952, *Howell 28552* (CAS); upper reaches of Toomey Creek above "Grand Canyon" of Inmaha River (near mouth of river) along Vance Drew Trail, bare stony slopes, 16 Jul 1950, *Kruckeberg 2304* (UC, WTU); Wallowa Mts, stony banks of Slickrock Creek, vicinity of Hurricane Creek, 16 Aug 1946, *Maguire & Holmgren 27045* (UC); sandy banks of Snake River Canyon, Johnson's Bar, 10 Jul 1943, *Murley 1716* (MO); Imnaha, dry ground, 4 Jun 1923, *Sherwood 434* (LL); Imnaha, 5 Jun 1923, *Sherwood 433* (LL). Wasco Co.: Mayer State Park, Rowena, banks of the Columbia River, common in sand and rocky sites, mostly below high water mark, 12 Aug 1981, *Chambers 4899* (Portland State image!); along I-84 ca. 4.6 mi W of Exit 97 at Celilo, hillside, sandy soil, 55 m, 5 Sep 2011, *Halse 8356* (SRP image!); The Dalles, Jun 1869, *Harford & Dunn s.n.* (UC); E of The Dalles, 29 Jun 1938, *Milburge 1471* (WTU); The Dalles, 7 Sep 1916, *Shantz & Piemeisel 6178* (LL); The Dalles, dry ground, 1 Jul 1927, *Thompson 2820* (DS); The Dalles, 4 Jul 1931, *Thompson 7199* (CAS). **Utah**. Cache Co.: Bear River Range, head of Crescent Lake Canyon, 1.5 mi W of Logan River, loamy sand, 9000 ft, 24 Jul 1981, *Neely 589* (BRY); Wasatch Range, Tony Grove Lake, NW ridge, limestone outcrops, 8200 ft, doug fir-aspen, 1 Aug 1982, *Thorne 2187* (BRY); S end of Cache Valley on ridge extending NE from James Peak, ca. 5.9 km SSE of the summit of Middle Mtn, ledges of S-facing quartzite outcrop, 9200 ft, 15 Jul 1997, *Windham 97-133*, **n=9** (MO). Daggett Co.: Carter Creek, 8000 ft, 4 Jul 1944, *Jensen s.n.* (IDS image!, UC; a dup of this sheet at WS is *H. incensa*). Duchesne Co.: Uintah Mts, Pole Mtn, Farm Creek Mtn, Whiterocks drainage, burned lodgepole pine area, 9920 ft, 27 Sep 2011, *Huber 5260* (BRY). Grand Co.: Ryan Creek, ca. 2 air mi due W of Renegade Peak, S exposure of canyon slope, pinyon-juniper, 5940 ft, 31 May 1984, *Atwood et al. 9810* (BRY, NY); San Miguel and Lower Dolores River Drainages, slopes above Buckhorn draw, granitic slopes with juniper and *Purshia*, 4900 ft, 26 May 1994, *Lyon 3439* (FLD, RM). Rich Co.: Bear Lake State Park, N side of Bear Lake, 5926 ft, 20 Jul 2006, *Moon 2083* (NY). Salt Lake Co.: Little Cottonwood Canyon, 1 mi below Tanners Flat, roadside, 6800 ft, 22 Jul 1961, *Allan 178* (BRY-2 sheets); Lake Blanche, Big Cottonwood Canyon, 9500 ft, 9 Jul 1935, *Cottam 6284* (LL); Little Cottonwood Canyon, roadside, 7500 ft, 18 Aug 1956, *Cottam 14526* (RSA); Big Cottonwood Canyon, among rocks in exposed places, 9100 ft, 5 Aug 1905, *Garrett 1585* (DS-2 sheets, NY, PH, RM); Mose Falls Trail, Big Cottonwood Canyon, 25 Jul 1940, *Garrett 8353* (UC); Wasatch Mts, Alta, 8000 ft, 14 Aug 1879, *Jones 1271* (MISSA image!, NY, POM); Salt Lake City, Aug 1883, *Jones s.n.* (POM); Big Cottonwood Canyon, 26 Aug 1928, *Kildale 6684* (DS-2 sheets); Brighton, below Twin Lake, rocky slopes, 9200 ft, 5 Aug 1939, *Maguire 17340* (NY); Big Cottonwood Canyon, 10,5000 ft, 14 Aug 1961, *Rowland 16976* (BRY); E of Midvale on Utah Hwy 190, Big Cottonwood Canyon, Mill B Picnic Area, Wasatch Natl Forest, cracks of exposed rocks, 7 Aug 1990, *Semple et al. 9247*, **2n=18** (BRY, MO); Wasatch Mts, vic. of Clayton Peak, 10,00 ft, 12-26 Aug 1903, *Stokes s.n.* (MO). Summit Co.: Rocky slopes just above Snydermill Lodge (E of Olympic ski jump, NNW of Park city), 6900 ft, drying loamy soil of crevices, 22 Jul 2008, *Anderson 23,057* (UTC image!); Kamas, dry rocky slopes, 7200 ft, 1916, *Brower 325x* (RM); Gogorza, 11 Aug 1908, *Garrett 2304a* (LL, NY, RM); East Canyon, Sep 1929, *Garrett 5466* (LL); East Canyon near Gogorza, dry hillside, 6300 ft, 15 Aug 1953, *Garrett 8631* (SMU, UC); just W of Gorgoza, along side of hwy [from Parley's Canyon to Evanston, Wyo.], 8 Aug 1945, *Garrett & Milner 8848* (RSA-2 sheets); Wasatch Mts, Smith & Morehouse Canyon, limestone ledges and cliffs, 8050 ft, 24 Aug 1984, *Goodrich 21436* (BRY, NY). Uintah Co.: Ca. 10 mi S of Bonanza on Hwy 45, common on sandy soil, 5600 ft, 25 Jul 1965, *Holmgren 2264* (NCSC, NY). Utah Co.: Mt. Timpanogos, dry summit, 11,000 ft, 2 Aug 1927, *Cottam 1336* (BRY); Upper Grove, 4 Aug 1925, *Garrett 3405* (NY); Wasatch Mts, Mt. Timpanogos, 22 Jun 1928, *Garrett 3887* (LL); Wasatch Mts, Mt. Timpanogos, 14 Aug

1930, *Garrett 5712* (LL); Cascade Mtn, cirque up Dry Fork, cliff crevices, 9600 ft, 17 Aug 1995, *Johnson 605* (BRY); American Forks, 26 Jul 1880, *Jones s.n.* (CAS, DS); American Fork, 28 Jul 1880, *Jones s.n.* (POM); Mt. Timpanogos, Aspen Grove, 6800 ft, 1 Jul 1949, *Murphy 60* (BRY); Aspen Grove [in Provo Canyon], creek bank, 6800 ft, 28 Jun 1939, *Ream 9297* (BRY, UC); American Fork Canyon, pass between Alpine and Granite Flat, 9400 ft, 12 Jul 1961, *Rowland 16887* (BRY); along trail to and at Stewarts Cascade, riparian and mixed mtn brush, 6600-6800 ft, 12 Sep 1980, *Welsh 633* (BRY, NY). Wasatch Co.: Deer Creek, 3 Aug 1880, *Jones 1271A* (POM). **Washington**. Asotin Co.: Along Snake River, 4 mi S of Asotin, sandy soil, 29 Jun 1958, *Baker 15234* (SRP image!). Ferry Co.: At Haag Cove on the Columbia River, 20 Jul 1973, *Saufferer 294* (BRIT, DS, NY, TEX, VDB); steep slope uphill side of Deadman Creek Rd, 1800 ft, 7 Aug 1995, *Swartz 129* (ID); slope below Deadman Creek Rd, 1400 ft, 17 Aug 1996, *Swartz 450* (ID). Klickitat Co.: White Salmon, gravel pit, 132 m, 17 Jul 1983, *Halse 2708* (WTU); 10 mi E of Bingen, base of basaltic cliff, 31 May 1946, *Hitchcock & Muhlick 13775* (WTU); S side of Dalles Airport, 200 ft, 23 May 2004, *Legler 1623* (WTU); ca 1 mi N of Dalles Dam on Hwy 97, dry sandy roadcut, 200 ft, 31 Aug 1960, *Munz 24228* (RSA, UC). Okanogan Co.: above Green Lake W of Omak, rocky hillside, 13 Aug 1931, *Fiker 466* (LL, WTU); Omak, 3 Jul 1911, *Jones s.n.* (POM); valley of Methow River, gravel bar of river, 21 Jul 1921, *St. John et al. 5518* (LL, UC); near Tonasket, dry open slopes, 2000 ft, 2 Jul 1932, *Thompson 8697* (MO, LL, WTU); near Tonasket, rocky sagebrush banks of Columbia River, 18 Jun 1935, *Thompson 11701* (CAS-2 sheets, LL, MO, PH, POM, WTU-2 sheets). Pend Oreille Co.: shores of Boundary Dam, Aug 1969, *Layser 1113* (WTU; × *H. vespertina*). Skamania Co.: S of Dalles Airport, loose and stabilized dunes and volcanic rock outcrops between runway and RR River, 16 Jun 2001, 262 ft, *Colwell 01-40* (ID, WTU). Spokane Co.: Spokane River, sand bar, 24 Sep 1913, *Johnson 2020* (WTU); near Spokane, 1912, *Nelson 60* (RM); by the Spokane River at Spokane Bridge, 14 Sep 1916, *Suksdorf 9061* (GH, WS); S side of Spokane, sandy soil on hills above jct of Hwys 10 and 195, 1 Jul 1941, *Weber 2234* (MO, NY, UC, WTU). Stevens Co.: Meyers Falls, RR embankment, 29 Jun 1903, *Beattie & Chapman 2198* (UC, WTU); Kettle Falls, dry sandy roadside, 2 Jul 1939, *Boner & Weldert 192* (CAS, DS, MO, NY, RM, UC, WTU); 3 mi NW of Northport, sandy alluvial soil, S slope, 1550 ft, 28 Jun 1932, *Hedgcock s.n.* (RSA); Myers Falls, sand 25 Aug 1902, *Kreager 516* (UC); Gold Creek at hwy, dry gravelly soil, *Purshia* association, 1900 ft, 5 Aug 1937, *Livingston s.n.* (BRY). Whatcom Co.: Ross Lake, mouth of Lightning Creek, S-facing cliffs, 3 Aug 1989, *Every & Vanbianchi s.n.* (WTU). Whitman Co.: Wawawai, Jun 1898, *Elmer 1017* (WTU). Yakima Co.: Yakima region, Oct 1883, *Brandegee 838* (UC). **Wyoming**. Albany Co.: Centennial-Rambler Road, gravelly slopes, 1 Sep 1903, *Goodding 2070* (DS, MO, RM); Sheep Mtn, near aspen groves, 2 Sep 1903, *Goodding 2079* (DS, MO, NY, RM, UC); Medicine Bow Mts, Medicine Bow Natl Forest, along Rd 517 SE of Albany, grassy meadow, 14 Jul 1991, *Keil 22283* (OBI, UC); Lookout, granite flats, 1 Aug 1913, *Macbride 2595* (MO, RM); Hermosa, deep pine woods, 3 Aug 1913, *Macbride 2601* (MO, RM); Cummins, 29 Jul 1895, *Nelson 1497* (MO, RM); Laramie Hills, ravines, 18 Sep 1890, *Nelson & Nelson 6851* (MO); Centennial, moist canyons, 7 Aug 1902, *Nelson 8814* (MO); Bacon's Ranch, river bottoms, 15 Aug 1903, *Nelson 8921* (MO, NY, RM, UC); Laramie Plains, 1 Jul 1909, *Nelson 9310* (MO, RM, UC); near Tie Siding, Sep 1897, *Osterhout 1327* (NY). Big Horn Co.: Red Bank, in the dryer meadows, 20 Jul 1901, *Goodding 331* (MO, NY, UC). Campbell Co.: South Pumpkin Butte, 5093 ft, 27 Jul 1978, *Dueholm 5057* (RM). Carbon Co.: Windy Ridge Rd, rocky grassland, 6800 ft, 19 Jul 2008, *Dorn 10509* (RM); Medicine Bow Mts, Cedar Ridge and Cottonwood Creek, ca. 3 air mi NW of Hwy 130-230 intersection, ca. 9 air mi SE of Saratoga, sagebrush at base of ridge, ca. 7050 ft, 22 Jun 2009, *Lukas 9126* [atypical in reduced capitular bracts] (BRY); Beaver Creek, along road to North Park, 18 Aug 1916, *Osterhout 5538* (RM). Fremont Co.: Sweetwater Rocks, Cranner Rock, 14.8 mi ESE of Jeffrey City, soil between granite boulders, 6280 ft, 13 Jun 1986, *Haines 6313* (NY); Split Rock Historical Marker site E of Jeffery City on Wyo Hwy 287, in soil pockets in cracks of gigantic outcrop, 26 Aug 1995, *Semple & Zhang 10417* (BRY, MO). Johnson Co.: E side Lake Desmet, sagebrush plain, 4800 ft, 21 Jul 1979, *Dueholm 8462* (RM); Big Horn Mts, Soldiers Park, 9000 ft, 19 Aug 1898, *Williams s.n.* (NY). Hot Springs Co.: Owl Creek

Mts, lower end of Wind River Canyon, along US Hwy 20/Wyo 789, 4 mi S of Thermopolis, rocky riparian, 4430 ft, 22 Jun 1997, *Evert 33231* (RM). Laramie Co.: 1.5 mi NW of Granite Reservoir, grassy hillside, 7400 ft, 12 Sep 1991, *Dorn 5318* (RM); Cherokee Park, rich most meadowlands, 30 Jul 1923, *Nelson 10007* (DS). Lincoln Co.: Salt River Range, along Greys River at Forest Park, ca. 16.5 air mi ESE of Thayne, 14 air mi NE of Afton, gravel soil of flood channel, 6900 ft, 13 Jul 1996, *Harrison 727* (RM). Natrona Co.: Rattlesnake Mts, Burnt Wagon Draw and N slope of range, limber pine-covered N slope with drainages and open slopes and flats, 6800 ft, 26 Jun 1981, *Fonken 1261* (MO); Platte River, rocky foothills, 27 Jun 1901, *Goodding 120* [x *H. hispida*?] (BRY); Seventeen Mile Well on Salt Creek Rd, sandstone hillsides, 8 Jul 1901, *Goodding 215* (DS-2 sheets, MO, POM-2 sheets, RM-2 sheets, UC). Park Co.: Bighorn Basin, along Co. Rd 7WC at Dry Creek, ca. 3 air mi WNW of Cody, riparian, 5200 ft, 17 Jul 2001, *Lum 879* (BRY); Yellowstone Natl Park, Gardiner River, dry stony river bottom, 19 Jul 1899, *Nelson 5967* (MO, NY); Cody, Shoshone Canyon, 15 Aug 1910, *Nelson 9552* (MO, RM, UC); Bighorn Basin, along Gooseberry Creek, ca. 10.5 air mi SSE of Meeteetse, clay slopes with sandstone outcrops and ledges, 6000 ft, 31 Jul 1983, *Nelson 10610* (BRY); Yellowstone Natl Park, Bechler Canyon, Three Rivers Jct, wet meadows along Gregg Littles Fork, pine-spruce-fir, 7225 ft, 29 Aug 1986, *Thorne 5033* (BRY). Platte Co.: T28N R68W Sect 14-23 line, sandy wash, 4600 ft, 12 Sep 1992, *Dorn 5376* (MO, NY, RM). Sheridan Co.: Sherman, gravelly ridges, 6 Aug 1901, *Nelson 8575* (MO); Big Horn Mts, soil crevices of granite rocks above Story, 13 Jul 1934, *Rollins 633* (MO). Sweetwater Co.: Rock Springs, dry prairie, 10 Jul 1942, *Degener & Peiler 16096* (MO, NY); Leucite Hills, dry ledges, 18 Jun 1901, *Merrill & Wilcox 508* (NY); Point of Rocks, rocky slopes, 12 Jun 1900, *Nelson 7157* (MO). Washakie Co.: foothills of W slope of Bighorn Mts, 0.25 mi NE of Choate, slopes on S side of Billy Creek, 6800 ft, 23 Aug 1993, *Fertig 14456* (RM).

7. HETEROTHECA SCELIONIS Nesom, **sp. nov.** **TYPE**: **Oregon**. Jackson Co.: E of Central Point, banks of the Rogue River at Bybee's bridge, dry gravelly places, 25 Jul 1918, *A.A. Heller 13080* (holotype: US-Fig. 24; isotypes: CAS, DS, MO, NY, PH-2 sheets, WTU).

Similar to *Heterotheca hirsuta* in its glandular surfaces with reduced non-glandular vestiture and its long-ciliate leaf and bract margins but different in its linear peduncular bracts, lack of capitular bracts and broader, more triangular phyllaries. Distinct from *H. orovillosa* in its less dense vestiture of longer non-glandular hairs, linear-bracteate peduncles, triangular phyllaries with glandular surfaces, and long-ciliate petiole margins.

Stems 25–40 cm, erect to ascending-erect, branching mostly above midstem, hirsute to hirsute-villous with spreading to deflexed non-glandular hairs, sparsely to densely minutely glandular. **Leaves** cauline, basal mostly withered by flowering, 2–3 cm long, oblanceolate with a petiolar base, largest at midstem, midstem oblanceolate to oblong-oblanceolate and becoming epetiolate, mostly 3–3.5 cm long, gradually decreasing in size distally, becoming linear and bracteate, leaf and bract surfaces loosely strigose to hirsute or hirsute-villous, at least the distal evidently sessile-glandular, petiole margins and at least proximal blade margins long-ciliate. **Heads** solitary on axillary branches 4–8 cm long, peduncles becoming linear-bracteate; capitular bracts absent. **Involucres** 9–12 mm wide (pressed); phyllaries narrowly triangular, shallowly keeled, in 4–5 series evenly graduate in length, longest 7–8.5 mm long, minutely glandular, without non-glandular hairs, medial area broad and darkened, margins narrow, whitish. **Ray flowers** 15–20, ligules ca. 10 mm long.

Flowering Jun–Aug. Sandy and rocky banks of creeks and rivers, 500–2400 ft. Known by collections from along the Applegate, Clearwater, Rogue, and Umpqua rivers and from Evans Creek, a tributary of the Rogue River.

The epithet ("of the rogue") alludes to the Rogue River, a major feature in the range of the species. The river's name supposedly originated with French fur trappers, who regarded native

Americans living along it as rogues. Latin pronunciation of the beginning "sc" of scelionis is "sh" as in shall.

Additional collections. **Oregon**. Douglas Co.: Sandy ground along Umpqua River, near Dillard, 13 Jul 1945, *Peck 23728* (POM); Clear Water, [no date], *Spalding s.n.* (MO). Jackson Co.: Evans Creek near Wimer, 22 Jul 1892, *Hammond 233* (MO, US-Fig. 25); no specific locality, 1917, *Hawkins s.n.* (MONTU, Fig. 26); along the Applegate River 2 mi S of Ruch, 25 Aug 1927, *Wolf 944* (DS, RSA). Josephine Co.: Rogue River 10 mi N of Grants Pass, 9 Jul 1926, *Abrams 11239* (DS); Woodville [now the town of Rogue River], Jun 1888, *Howell 1805* (HPSU); Grant's Pass, 17 Jun 1909, *Howell 1806* (HPSU, Fig. 27); Grant's Pass, 17 Jun 1909, *Howell 1807* (HPSU, Fig. 28); Rogue Canyon, 3 mi below Galice, sandy along river, 850 m, 4 Jul 1948, *Ripley & Barneby 9625* (CAS).

Heterotheca scelionis varies in density of vestiture but the otherwise morphological and geographic cohesiveness and consistency of ecology support its recognition. The species overlaps in distribution with *H. oregona* in Douglas and Josephine counties but it otherwise is not sympatric with any other goldenaster.

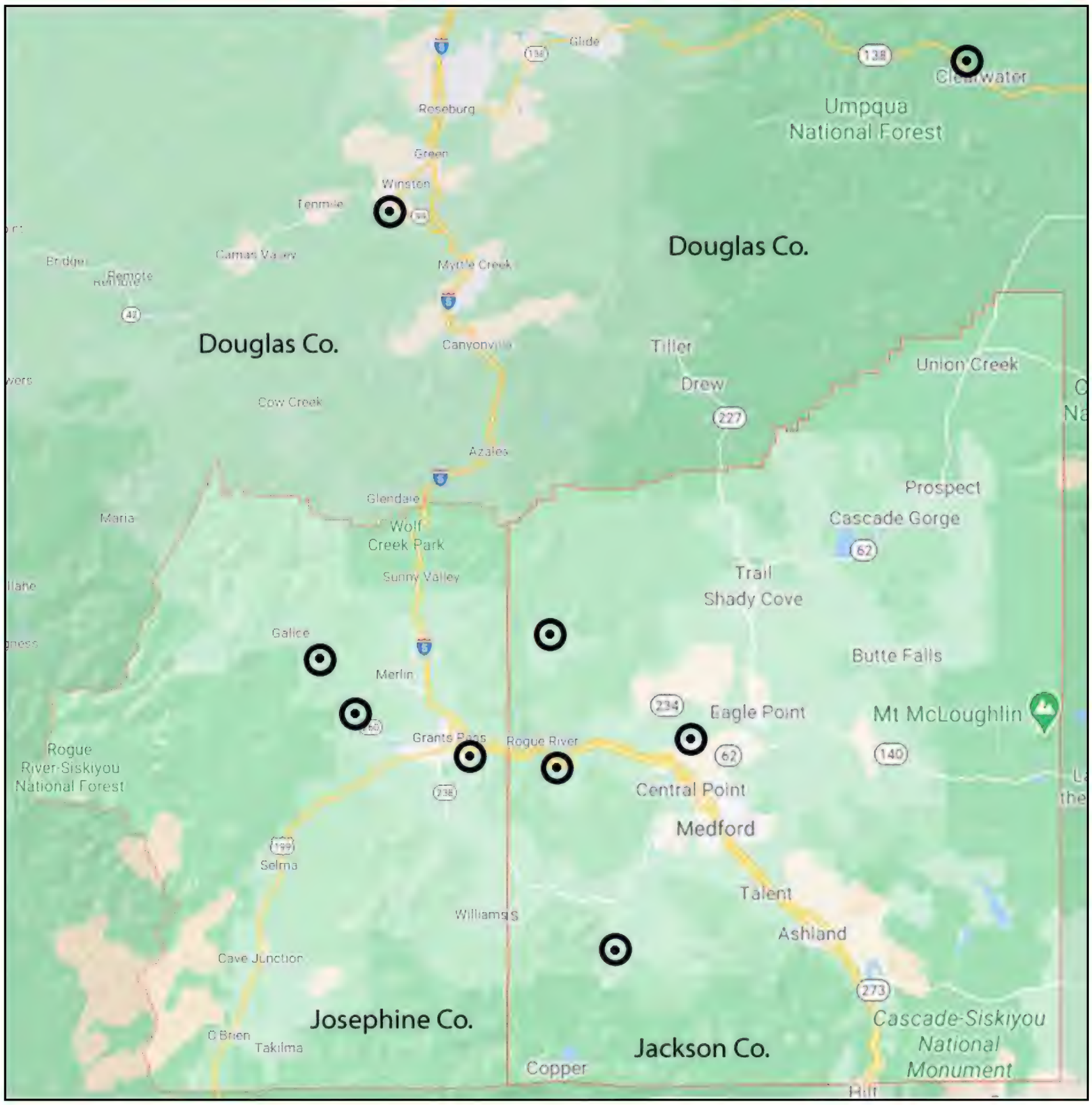


Figure 23. Distribution of *Heterotheca scelionis*. Douglas, Jackson, and Josephine counties, Oregon.

Figure 24. *Heterotheca scelionis*. Jackson Co., Oregon. Holotype (US).

Figure 25. *Heterotheca scelionis*. Wimer, Jackson Co., Oregon. *Hammond 233* (US).

Figure 26. *Heterotheca scelionis*. Jackson Co., Oregon. *Hawkins s.n.* (MONT).

Figure 27. *Heterotheca scelionis*. Grant's Pass, Josephine Co., Oregon. *Howell 1806* (HPSU).

Figure 28. *Heterotheca scelionis*. Grant's Pass, Josephine Co., Oregon. *Howell 1807* (HPSU).

8. HETEROTHECA VESPERTINA Nesom, **sp. nov. TYPE**: **Washington**. Chelan Co.: Sandbars of Columbia River at Entiat [at mouth of Entiat River], 28 Jun 1934, *J.W. Thompson 10809* (holotype: MO!; isotypes: DS-2 sheets, LL, POM, US-Fig. 30, WTU-2 sheets).

Similar to *Heterotheca villosa* sensu stricto in its strigose, often silvery-sericeous stems and leaves but distinct in its lack of capitular bracts, broader involucres, fewer ray flowers, and different geography.

Perennials from a thick, woody taproot. **Stems** erect, (10–)15–40 cm tall, vestiture all strigose with appressed hairs or understory appressed with spreading overstory hairs, eglandular. **Leaves** usually ascending, narrowly to broadly oblong-oblanceolate or oblanceolate, epetiolate, not clasping, or sometimes proximal petiolate, mostly 2–4 cm long, relatively even-sized along the stem or sometimes smaller approaching the inflorescence, strigose with closely appressed hairs, sometimes silvery-sericeous, margins usually eciliate, sometimes long-ciliate or sometimes ciliate only along proximal margins. **Heads** solitary or in close clusters on bracteate peduncles 10–30 mm long, with narrow peduncular or subpeduncular bracts often as long as or longer than the involucre, without capitular bracts. **Involucres** (8–)11–15 mm wide (pressed), inner phyllaries 7–9 mm long; phyllaries strigose to strigose-sericeous with loosely appressed hairs, eglandular, tips not differently colored. **Ray flowers** (8–)14–16. Chromosome number, 2*n*=18 (*Semple 2001*, *2002*, Nez Perce Co., Idaho; *Semple & Brouillet 7082*, Klickitat Co., Washington; *Chinnappa & Chmielewski 257*, Alberta; *Taylor & Taylor 5342*, British Columbia).

Heterotheca vespertina is characterized by its large, often solitary (long-pedunculate) heads, inconsistently produced capitular bracts, and appressed cauline and leaf vestiture of fine-based hairs, usually giving plants a silvery-sericeous aspect. It is similar in vestiture to *H. villosa* but the two entities are allopatric — they perhaps are an evolutionarily vicariant pair but convergence is common in *Heterotheca* and their relationship is speculative. Although both entities are variable over their relatively wide ranges, *H. vespertina* differs consistently from *H. villosa* in its lack of prominent capitular bracts, broader involucres, and fewer ray flowers. Their allopatry is significant in the recognition of *H. vespertina* as distinct.

1. Heads usually in a compact corymboid arrangement, capitular bracts present; involucres 7–12 mm wide (pressed), inner phyllaries 6–8 mm long; ray flowers 16–28; phyllary tips often purplish ..... 11. **Heterotheca villosa**

1. Heads solitary (long pedunculate) or in a loosely corymboid arrangement; capitular bracts present or absent; involucres (8–)11–15 mm wide (pressed), inner phyllaries 7–9 mm long; ray flowers (8–)14–16; phyllary tips not colored ..... 7. **Heterotheca vespertina**

Additional collections examined. **CANADA**. **British Columbia**. Jackman Flats, ca. 110 km on the Jasper-Kamloops road, sandy soil with open lodgepole pine forest, 600 m, 14 Aug 1997, *Breteler 13887* (MO); E side of Kootenay Lake near Sanca Creek, open, rocky, W-facing cliffs, 18 Jun 1953, *Calder & Savile 9345* (CAS, ID, WTU); W side of Okanogan Lake, 26 Jun 1953, *Calder & Saville 9699* (NY, WTU); Ashcroft, 28 Jun 1907, *Cowles 206* (MO); Lytton, 16 Jul 1899, *Diehl s.n.* (BRY); Ashnola River Road (km 7), open *Pinus ponderosa*, gravel floodplain, 900 m, 29 Jun 1980, *Douglas 11661* (BRY); Glacier, Jul 1896, *Dudley s.n.* (DS); 2 mi N of Lytton (jct of Fraser and Thompson rivers), bone-dry banks and cutting of dry river bench, 21 Jun 1933, *McCabe 187* (UC); Skagit River, 17 Jun 1905, *Macoun 76937* (NY). **USA**. **Idaho**. Clearwater Co.: 6 mi NE of Ahsahka, gravelly banks of the N Fork Clearwater River, 11 Jul 1946, *Christ & Smith 15408* (NY). Idaho Co.: 2 mi S of Pollock along the Little Salmon River, 21 Jul 1954, *Baker 11975* (WTU); Riggins, rock outcrop along Salmon River, 5 Aug 1937, *Christ 8499* (NY) and *8500* (NY); 1.5 mi below Kooskia, sandy flat near Clearwater River, 31 May 1936, *Constance & Rollins 1697* (WS, WTU); White Bird, 20 Jun 1939, *Davis 959* (RM, UC); Spring Bar on Salmon River Road, 7.5 air mi E of Riggins, sandy margin of dried river bed, 5 Oct 2013, *Ertter 21688* (UC); Goff, 1700 ft, Dec 1899, *Jones s.n.* (POM); 1.6 mi E of Slate Creek up Slate Creek road, dry rocky hillside with

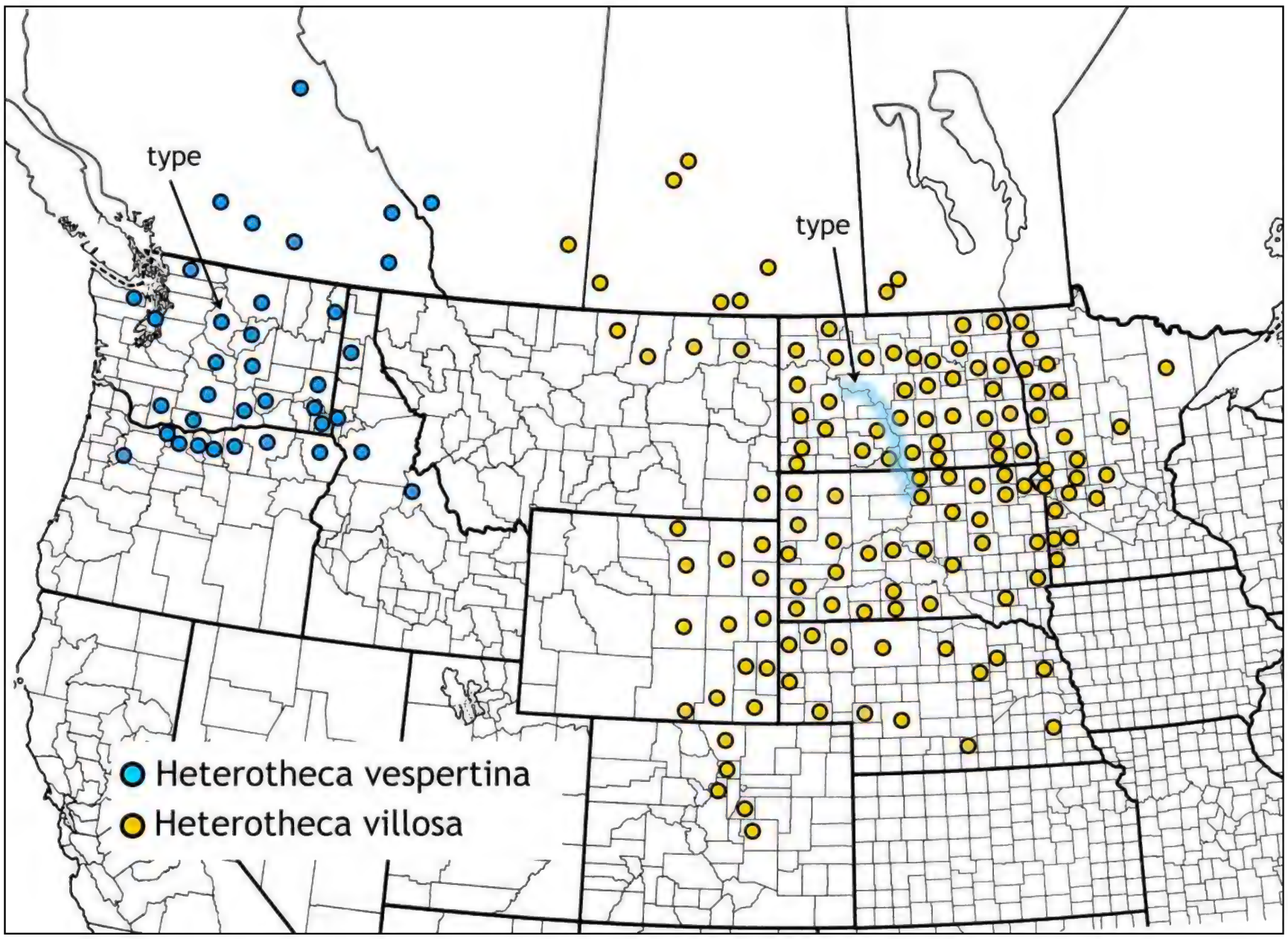


Figure 29. Distribution of *Heterotheca vespertina* and *H. villosa*. Blue highlight shows stretch of Missouri River along which the type collection was made (see Nesom, Phytoneuron 2020-67).

Figure 30. Detail from isotype (US).

Figure 31. *Heterotheca vespertina*, Benton Co., Washington. *Sackschewsky 156* (PNNL).

Figure 32. *Heterotheca vespertina*, Island Co., Washington. *Legler 1692* (WTU).

Opuntia, 28 Jun 1950, *Jones 125* (DS, NY, RSA, SMU, WS, WTU); Middle Fork Clearwater, near Three Devils Creek, sand bar, 17 Aug 1950, *Jones 363* (WTU); 2.3 mi S of Slate Creek, sandy bench, 1800 ft, 12 Jul 1951, *Pringle 74* (ID). Kootenai Co.: Rocky places, Aug 1892, *Sandberg 5067* (POM, WTU). Lemhi Co.: Near mouth of Jacks Creek along Middle Fork Salmon River, flat rocky area, 3560 ft, 2 Jun 1992, *Mancuso 651* (ID). Nez Perce Co.: Lewiston, gravel bar in river, 16 May 1934, *Christ 4260* (NY); Lewiston, sandy river bank, 6 Jul 1913, *Dunkle 299* (ID); lower level adjacent to Clearwater, riparian, alluvium, 775 ft, 23 Aug 2000 *Foster 11997* (BRY); Craig Mtn, along the lower Salmon River, sand bar near mouth of China Creek, 29 Jun 1994, *Mancuso 1195* (ID); island near mouth of Clearwater, gravelly soil, 12 Oct 1924, *Ridout s.n.* (WS); E of Lewiston, just W of US Hwy 95 and US 12 junction, 22 Aug 1975, *Semple 2001* (MO-2 sheets); 17 mi NW of Orofino, rest area on US Hwy 12 between Lewiston and Orofino, 22 Aug 1975, *Semple 2002* (MO); Upper Ferry, Clearwater River, E of Lewiston, 31 May 1892, *Sandberg Exped. 280* (DS, NY-2 sheets, PH). **Oregon**. Gilliam Co.: Quinton, cliffs along the Columbia River, 250 ft, 27 Aug 1941, *Rose 41416* (CAS). Hood River Co.: Hood River, 10 Aug 1928, *Suksdorf 3399* (RM, RSA, WS [x *H. hirsuta*?], WTU-2 sheets); along I-80, W of The Dalles, 0.1 mi E of milepost 92, 8 mi W of the Sherman Co. line, roadside S of the freeway, 5 Aug 1983, *Sundberg 2032* (TEX, WTU). Marion Co.: 1.5 mi W of Orville, gravelly shore of Willamette River, 12 Jul 1922, *Nelson 4399* (WS, WTU); 1 mi S of Talbot, gravelly woods along Santiam River, 2 Aug 1922, *Nelson 4536* (WS); 2 mi W of Keizer, gravelly shore of Willamette River, 12 Aug 1922, *Nelson 4613* (PH). Multnomah Co.: Portland, dry areas, 3 Aug 1936, *Demaree 13411* (NY). Polk Co.: 1.5 mi N of West Salem, gravelly shore of Willamette River, 29 Jul 1923, *Nelson 4902* (PH). Sherman Co.: Near Biggs, Columbia River, 16 Jul 1923, *Peirson 3892* (RSA); mouth of Deschutes River, 13 May 1923, *Sherwood 418* (LL). Umatilla Co.: S bank Columbia River at Corps of Engineers Coldstream Park, E of Hat Rock State Park, dry river bank, 350 ft, 13 Sep 1982, *Grable 9646* (WS). Wallowa Co.: Snake River Canyon, Christmas Creek, dry slopes near river, 1035 ft, 11 Jun 1937, *Packard 236* (UC, WS). Wasco Co.: 15 mi NE of The Dalles, 14 Aug 1941, *Brenckle & Shinners 230* (PH); along Columbia River E of The Dalles, 10 Aug 1936, *Milburge 1257* (WTU); The Dalles, dry exposed slope, 26 Jun 1925, *Munz 9906* (POM); bank of John Day River at Clarno, 3 Jul 1921, *Peck 10011* (DS-2 sheets). Wasco/Sherman Co.: Bank of Columbia River at mouth of Deschutes River, 28 Jun 1921, *Peck 9927* (RSA). **Washington**. Asotin Co.: 4 mi S of Asotin, along Snake River, sandy soil, 29 Jun 1958, *Baker 15234* (ID, NY-2 sheets, WTU); 3 mi S of Asotin, gravel and sand bar of Snake River, 26 May 1944, *Hitchcock & Muhlick 8337* (NY, WS, WTU). Benton Co.: Roadside W of Midway, base of Umtanum Ridge, rocky soil, ca. 400 ft, 18 Jun 1983, *Baird 204* (BRY, NY); Hanford Works (DOE), disturbed area with rabbitbrush, 395 ft, 7 Jun 1984, *Baird 997* (BRY, NY); along Columbia River, 1 mi N of E White Bluffs ferry site, riparian, 380 ft, 13 Jun 1984, *Baird 1087* (BRY, NY); ca. 1/4 mi SE of Hanford reactor, above river, 9 Jul 1991, *Sackschyewsky 156* (BRY). Chelan Co.: Meyers Falls, 22 Aug 1902, *Kreager 516* (NY); near Leavenworth, just outside Wenatchee Natl Forest, 9 Aug 1938, *Purer 7757* (MO); rocky banks of the Columbia River at Entiat, 16 May 1931, *Thompson 6368* (MO, PH); rocky banks of the Columbia at Entiat, 25 Jun 1931, *Thompson 6899* (DS, LL, MO, PH, WTU-2 sheets). Clallam Co.: Eastern shore of Washington Harbor, steep sand bank above beach, 14 Sep 1921, St. John 5869 (MO). Franklin Co.: 8 mi N of Kahlotus, partially compacted sand between dunes, sandhills, 7 Jul 1935, *Constance & McMurray 1138* (LL, MO); Fish Hook Ferry, 210 m, 18 Sep 1894, *Leiberg 931* (UC). Garfield Co.: Glendale Bar, Snake River, 19 Jun 1892, *Henderson s.n.* (WTU); 4 mi below Lower Granite Dam of Snake River, sand dunes, 19 Jul 1983, *Jenkins SD-1* (WS); Illia, 25 Jun 1892, *Lake & Hull 752* (WS); 5 mi NE of Central Ferry, gravel bar, 31 May 1925, *St. John et al. 6984* (WS); Ilia, gravelly river bank, 23 Oct 1927, *St. John et al. 9231* (LL, WS). Grant Co.: Gopher Island of Columbia River, E of Ginkgo Petrified Forest State Park, 24 Jun 1936, *Smith 1243* (DS) and 15 Aug 1936, *Smith 2003* (DS). Island Co.: Whidby Island, between Ebey's Landing and Perego's Lagoon, 15 ft, 20 May 2001, *Beck 200120* (WTU); Whidby Island, Jul 1896, *Gardner s.n.* (UC); Glendale, 19 Jul 1892, *Lake & Hull s.n.* (MO); Whidby Island, Ebey's Landing, bluff 1/4 mi N of parking area, 7 ft, 4 Jun 2004, *Legler 1692* (WTU); Whidbey Island, scattered on sandy, grassy slope near salt water, 19 Jun 1983, *Naas 4218* (BRIT); ca. 3.5 mi W of Coupeville, sandy bluff, 7 Jul 1990, *Naas 5579* (WTU). Kittitas Co.: Yakima River, 24 Jul 1923, *E. Nelson s.n.* (RM); Rock Island, sandy plains, 610 ft, 14 Jul 1893, *Sandberg & Leiberg 454* (CAS, MO, NY, UC, WS); Ginkgo State Park, Gopher Island, 24 Jun 1936, *Smith 1243* (WTU); Ginkgo Petrified Forest State Park, Columbia River, 19 Jul 1936, *Smith 1375* (SMU, WS);

Ellensburg, 18 Jul 1897, *Whited 575* (WS). Klickitat Co.: Outlet of Rock Creek into Columbia River, N side of Hwy 14, 4 Jun 1980, *Camp 401* (WTU); Goldendale, prairies, 21 Jun 1926, *Gorman 7717* (DS); Bingen, 9 Aug 1926, *Jones 2427* (WTU); Columbia River, dry grounds, 25 Aug 1882, *Suksdorf s.n.* (MO, PH); near Columbus, 10 Jun 1886, *Suksdorf 2376* (WS); sand drifts at North Dalles, sagebrush region, 29 Jul 1934, *Thompson 11111* (LL). Okanogan Co.: Orville, 26 Jun 1911, *Jones s.n.* (POM); Methow River, gravel bar, 21 Jul 1921, *St. John et al. 5518* (WS, WTU). Pend Oreille Co.: Box Canyon, stony bank of Pend Oreille River, 3 Aug 1902, *Kreager 397* (UC, WS, WTU). Skamania Co.: Dalles of the Columbia, 2 Aug 1880, *Engelman s.n.* (MO). Walla Walla Co.: Fish Hook ferry, 210 m, 18 Sep 1894, *Leiberg 931* (NY). Whatcom Co.: Ross Lake Natl Rec Area, Lightning Creek Trail, ca. 1 mi above Ross Lake, 2400 ft, 14 Jul 2002, *Legler 43* (WTU). Whitman Co.: Snake Canyon E of Steptoe Canyon, crumbly basalt, 9 Jul 1964, *Daubenmire 6410* (WS); Snake River Canyon opposite Clarkston, Aug 1934, *Clarke s.n.* (WTU); Wawawai, 8 Jul 1898, *Piper s.n.* (NY, WS); Snake River, Indian, sandy bank, 20 May 1923, *St. John & Warren 3396* (NY, UC); alluvial fan entering Snake River, 0.2 mi E of USGS Gaging Station, 2 Jun 1965, *Wakefield 671* (WS, WTU). Yakima Co.: S bank Naches River, near confluence of Yakima River, ca. 40 ft, 3 Oct 1992, *Gage & Rodman 855* (WTU); Naches River, E of Naches town, 15 Oct 1942, *Hoover 6001* (CAS, OBI); near Yakima, 17 Jul 1927, *Jones 1792* (WTU); N Yakima, Aug 1895, *Watt s.n.* (WS).

9. HETEROTHECA OROVILLOSA Nesom, **sp. nov.** **TYPE**: **California**. Plumas Co.: Marble Mts, 4 Aug 1939, *Howell 15049* (holotype: UC; isotype: CAS).

Distinct in its caespitose habit, hirsute (1-storied vestiture) stems, mostly oblanceolate and essentially epetiolate leaves, solitary or loosely arranged heads on relatively long, bracteate peduncles without capitular bracts, and northeastern California-southwestern Oregon geographic range.

Perennials from a thick, woody taproot, sometimes with woody, rhizome-like caudex branches. **Stems** erect-ascending from the base, 10–40 cm, eglandular to evenly and densely sessile-glandular, sparsely to densely hirsute to hirsute-villous with curving, spreading to spreading-ascending or deflexed non-glandular hairs in a single story. **Leaves** evenly distributed up to the peduncles, mostly oblanceolate or oblong-oblanceolate to narrowly obovate or oblong-lanceolate, without a distinct petiolar region, 1.1–3 cm x (1–)2–8(–10) mm, mostly even-sized, sparsely to moderately hirsute-strigose, hirsute-villous, or pilose at least along the midvein, usually densely sessile-glandular to stipitate-glandular (especially adaxially), sometimes eglandular, margins ciliate proximally. **Heads** solitary or loosely arranged on relatively long (2–8 cm), bracteate peduncles, usually without capitular bracts or sometimes (especially in El Dorado, Placer, Sierra cos.) with 1-2 linear to linear-lanceolate bracts. **Involucres** 9–18 mm wide (pressed), inner phyllaries 7–10 mm; phyllaries finely loosely strigose to strigose-hirsute or villous-hirsute, sometimes sparsely so, eglandular to minutely sessile-glandular, margins prominently hyaline. **Disc corollas** glabrous. **Ray flowers** 9–24. **Chromosome numbers**, $2n$=18 (Plumas Co., *Suripto & Ahmed 9313*, as cited by Semple 2008), $2n$=36 (Shasta Co., *Semple & Suripto 5715*).

Flowering Jun–Aug(–Sep). Along rocky stream and lake sides, meadows, low alkaline areas, roadsides and roadbanks, rock outcrops, cliffs and rock crevices, lava beds, fir and mixed conifer, pine-fir, yellow pine, juniper-sagebrush, sagebrush scrub; (1200–)3600–8200(–8650) ft. California, sw Oregon (Josephine Co.), nw Nevada (Washoe Co.).

These plants previously have been identified as expressions of a broadly conceived *Heterotheca villosa* but they form a geographically discrete population system not sympatric with any other similar species. The southward-disjunct populations in Kern County appear to belong with the species.

Early in the study I thought two species existed among these plants and annotated some collections as "H. doradoensis" based on the strongly expressed glandularity of stems and leaf surfaces, but geographic patterns in vestiture are not evident *Heterotheca orovillosa* apparently varies widely in glandularity as well as in ecology.

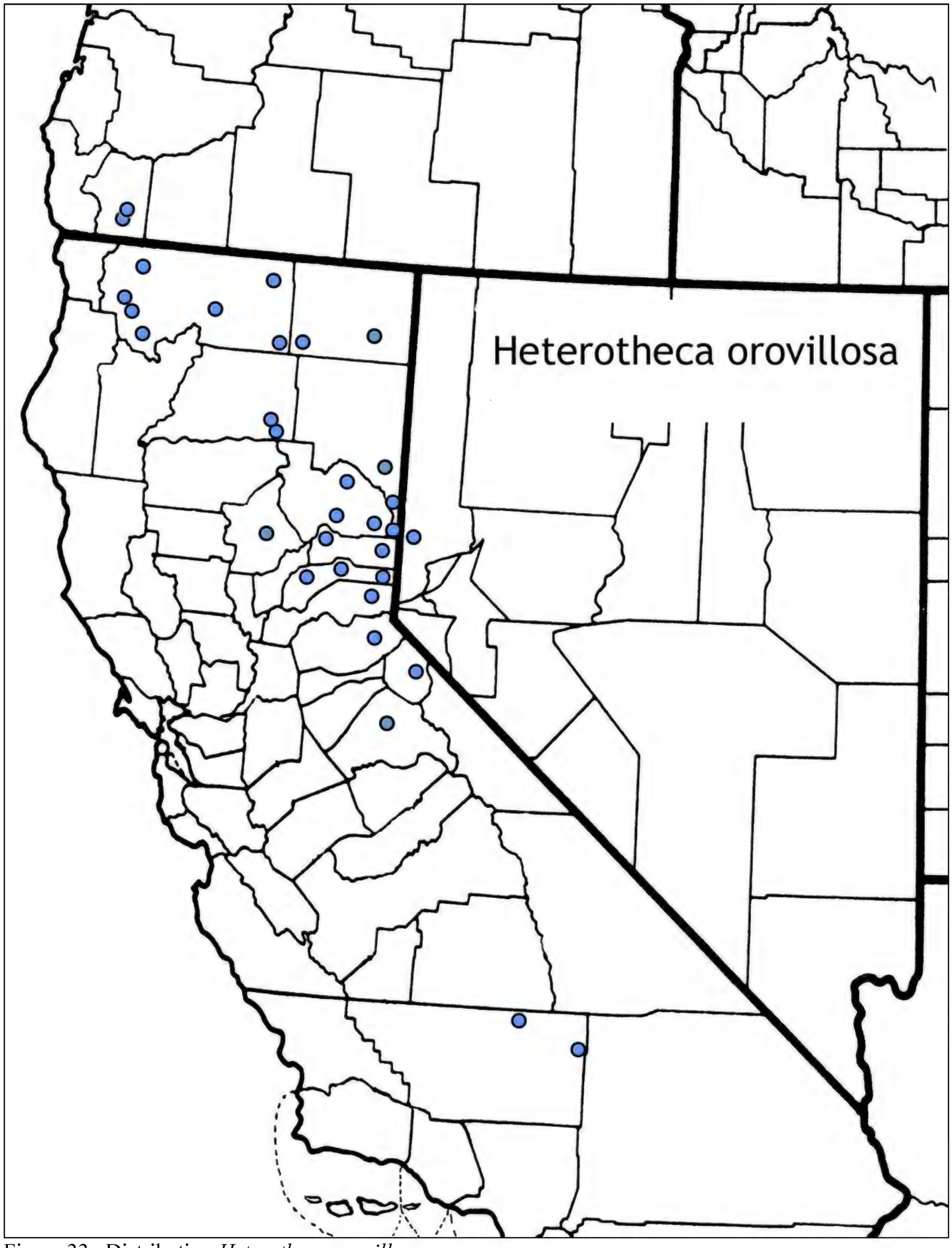


Figure 33. Distribution *Heterotheca orovillosa*.

Figure 34. *Heterotheca orovillosa*, Plumas Co., California.

Figure 35. *Heterotheca orovillosa*, Tuolumne Co., California. *Colwell AC05-299* (UC).

Figure 36. *Heterotheca orovillosa*, Siskyou Co., California. *Howell 15049* (UC).

Figure 37. *Heterotheca orovillosa*, Plumas Co., California, roadside on N side of Chilcoot, locality of Nesom *CA2017-7*. Upper: Single plant, many decumbent-ascending stems. Lower: Population aspect. Photos by Nesom, 22 Jul 2017.

Additional collections examined. **California**. Alpine Co: stream between Raymond Lake and Pleasant Valley, ca. 6000 ft, granite, sand, 11 Aug 1970, *Hardham 17711E* (CAS, TEX); N side of Pigeon Flat, 23 Jul 1939, *Hoover 4154* (LL, UC-2 sheets); Dixon Mine, ca 4 mi up Wolf Creek from E Fork of Carson River, 19 Jul 1959, *Wilkey s.n.* (CAS). El Dorado Co.: Lake Tahoe Region, Lake Valley, 6400 ft, 27 Jul 1911, *Abrams 4786* (DS, NY, UC); Heather Lake, crevices in granite, 8200 ft, 15 Aug 1930, *Abrams 12737* (LL, MO, SMU, WTU); Emerald Bay, Jun-Jul 1912, *Geis 60* (UC); Heather Lake, 7900 ft, 28 Aug 1918, *Jepson 8179* (JEPS, VDB); vicinity of Fallen Leaf Lake, summer 1923, *Lorraine s.n.* (DS); near foot of North Trail to Tallac, on rocks a few feet above the lake, 6400 ft, 15 Jul 1925, *Peirson 6283* (DS, POM); between Wright's Lake and Crystal Basin, SE of Four Cornered Peak, *Pinus jeffreyi* and *Abies concolor*, 6100 ft, 7 Sep 1970, *Stebbins 7093* (CAS). Kern Co.: 5 mi NW of Searles Station, 3500 ft, 10 May 1947, *Benson 12375* (POM); "Chico Rancheria" just N of Bull Run Creek, 1 mi NW of Kernville, sandy soil beside trail after creek crossing, 3000 ft, 31 Oct 1976, *Luthey 464* (CAS). Lassen Co.: Honey Lake Valley, ca. 5 mi W of Doyle on US 395, just inside Plumas Natl Forest boundary, open understory of pines, 9 Jun 1993, *André 19697* (UCR); Long Valley, Honey Lake Valley, 17-24 Jun 1897, *Burtt Davy s.n.* (UC); ca 3/4 mi ENE of Beckwourth Pass at end of old crumbly paved road, meadow at head of streamlet in sagebrush zone, ca 5000 ft, 24 Jul 1987, *Ertter 7302* (NY, RSA, UC); along state Hwy 70 at Beckwourth Pass, 1.6 mi E of Sierra Valley, 1584 m, 26 Aug 2010, *Halse 8091* (BRY, NY, RSA ID); Chat [2 mi ESE of Beckwourth Pass], 12 Jul 1897, *Hillman s.n.* (POM); Chat, 5000 ft, 18 Jun 1897, *Jones s.n.* (MO, POM); intersect. of Hwy 70 and Scott Road, 2.2 mi W of Hwy 395, roadside bank, sagebrush scrub, 4800 ft, 25 Jul 1990, *Oswald & Ahart 4397* (MO, UC); Ft. Sage Mts, big sage, decomposed granite, 5400 ft, 28 Jun 1982, *Schoolcraft 735* (NY); W of Hwy 395 and S of Hwy 70, near Hallelujah Junction, 4900 ft, 27 Jul 1974, *Williams 74-61-61* (CAS, TEX). Modoc Co.: lava beds at W side of Egg Lake, 1300 m, *Pinus ponderosa*, 6 Jul 1991, *Bartholomew 5980* (CAS); lava beds of SW part of the county, 21 Jun 1903, 4000 ft, *Hall & Babcock 4237* (UC). Nevada Co.: ca. 5 mi N of Nevada City, large rocks along along South Fork Yuba River, 2.5 mi E of the bridge, E of Lake Vera Road, foothill woodland, 400 m, 22 Aug 1983, *Ahart 4343* (CAS, MO); N side of Bowman Lake, rocks along dirt road, 5680 ft, 23 Oct 1986, *Ahart 5412* (CAS, MO); below Floriston granite soil, 5000 ft, 27 Jun 1933, *Benson 4564* (POM); along and near Interstate Hwy 80 at Farad Interchange, 5200 ft, 10 Oct 1976, *McPherson 76-31-2* (CAS); road paralleling the N side of Bowman Lake, ca 5 air mi E of Graniteville, fir forest, 5640 ft, 20 Aug 1998, *Oswald & Ahart 9513* (JEPS); Soda Springs, 19 Sep 1882, *Pringle s.n.* (CAS, SMU); on Nevada/Calif. state line, Jul 1888, *Sonne 465* (MO); old shingle mill near state line, Jul 1888, *Sonne s.n.* (UC-2 sheets); near Verdi, at Shingle Mill, Jul 1888, *Sonne s.n.* (UC); Lang's Crossing on S. Yuba River, Bear Valley-Bowman Rd, 4500 ft, 20 Sep 1962, *True 1098* (CAS) and *1099* (CAS); N shore of Bowman Lake, ca 11 mi N of Emigrant Gap, crevices in granite, 5600 ft, 27 Aug 1964, *True 1679* (CAS); Truckee River at Farad Powerhouse, dry rocky slope, 5200 ft, 30 Jun 1965, *True 2088* (CAS); ca 6 mi W of Truckee just S of Hwy 80 on Donner Lake Road, Negro Canyon, roadcut, 6700 ft, 23 Jun 1966, *True 2940* (CAS). Placer Co.: Donner, Jul 1889, *Brandegee s.n.* (UC); [no other data], Sep 1892, *Carpenter s.n.* (UC). Plumas Co.: W side of Little Last Chance Creek, on the strand of Frenchman Lake, mtn meadow in yellow pine forest, 5580 ft, 29 Aug 2001, *Ahart 9269* (JEPS); along US Hwy 40A, 6 mi E of Portola, abundant in field with sagebrush, 4825 ft, 3 Aug 1962, *Barclay et al. 1516* (LL); Plumas Natl Forest, 2.4 mi S of Johnsville or 7.8 mi S of Hwy 89 and road to Eureka State Park, just W of Eureka State Park, frequent on rocky slopes, greenstone rocks, 5440 ft, 13 Jun 1976, *Denton 3882* (WTU); NW edge of Sierra Valley, ca. 3.9 air mi E of Portola, Beckwourth-Calpine road (A23), roadside of disturbed dry meadow in sagebrush scrub, 4885 ft, 8 Aug 2003, *Dittes 2003-80* (RSA); Frenchman Lake, Plumas Natl Forest, 5670 ft, roadside, 22 Aug 1989, *Goeden 1* (UCR); Indian Valley, 3600 ft, Jul 1903, *Hall & Babcock 4435* (DS, RM, UC); Sierra Valley, Hindoo Ranch, roadside, 4890 ft, 29 Jun 1989, *Harnach 201* (CAS); Jamison Creek, ca 6000 ft, 27 Jun 1951, *Howell 27632* (CAS); Vinton, Sierra Valley, 5000 ft, 20 Aug 1951, *Howell 28230* (CAS); Sierra Valley near Beckwourth, ca. 4900 ft, 25 Sep 1959, *Howell 35011* (CAS); canyon of Little Last Chance Creek between Chilcoot and Frenchman Reservoir, 5500 ft, 11 Aug 1977, *Howell 52670* (CAS, UCR); near Cascade Creek, ca 1.25 mi SW of Little Grizzly Creek, edge of dirt road, 6100 ft, 15 Aug 1990, *Janeway 3829* (CAS); S-most end of Diamond Mts ca. 4.5 N of Beckwourth Pass, E-facing slope of soft, decomposed granite soil, 30 Jul 2005, *Janeway 8502* (RSA); dirt road on N side of Jamison Creek 0.3 road km W of Plumas Eureka State Park boundary, N side (upslope) of road, 1704 m, 6 Aug 2011, *Janeway*

10629 (RSA); Genesee Valley, 3600 ft, 16 Aug 1918, *Jepson 8022* (JEPS); Rich Point, Middle Fork Feather River, rocky river bed, 3000 ft, 22 Jul 1924, *Jepson 10609* (JEPS); Sierra Valley, just S of Vinton, wet meadow area, 5000 ft, 16 Jun 1983, *Lavin 4419* (CAS, MO, TEX); N side of Chilcoot along Hwy 70, sagebrush plains in Sierra Valley, 5000 ft, with *Grindelia* and *Gutierrezia*, just into full flower, very abundant from here west to Vinton, each plant multicipital with 10-20 decumbent-ascending stems from a woody taproot, 22 Jul 2017, *Nesom CA2017-7* (ARIZ, CAS, COLO, MO, OSU, RSA, RM, TEX, UC, US, WTU); Chilcoot, Sierra Valley, 4995 ft, 23 Jul 1934, *Rose 34419* (CAS, WTU); Vinton, low alkaline area among sagebrush, ca 4940 ft, 19 Jul 1955, *Rose 55150* (CAS, RSA); SW of Portola, loamy soil with *Pinus jeffreyi*, *Artemisia tridentata*, *Purshia tridentata*, 4860 ft, 17 Jun 1981, *Schoolcraft 469* (UC); couple of mi N of Chilcoot, sandy slopes and flats with big sagebrush, 5000 ft, 27 Jul 1982, *Schoolcraft s.n.* (UC); N of Chilcoot, sagebrush, 5400 ft, 27 Jul 1982, *Schoolcraft 814* (NY); E side of Ramelli Ranch, S of Feather River, ca 2 mi ESE of Beckwourth, sagebrush scrub, dry sandy soil, 4800 ft, 13 Jul 1981, *Taylor 4005* (MO); Wemple Cabin, Antelope Creek, 1 air mi NE of Antelope Lake, shoulder of gravel road edge of sagebrush meadow, 6100 ft, 12 Aug 2000, *Taylor 17550* (JEPS); ca 3 mi SW of Johnsville, ca. 1 mi W of Plumas-Eureka State Park, along N side of Jamison Creek Road (507) on cliffs, 5900 ft, 11 Aug 1982, *Taylor & Swanson 4970* (CAS, MO); near Chilcoot, 5000 ft, 23 Jul 1974, *Williams 74-P-1* (CAS, NY). Shasta Co.: Lassen Natl Forest, lava flats ca 1.5 mi ENE of Sugarloaf Peak, 1303 m, 19 Jun 2011, *Baniaga 380* (OBI, UC); Upper Falls River Valley, 3400 ft, 11 Aug 1914, *Jepson 5783* (JEPS); 1 mi E of Old Station on Hwy 44, base of large lava flow where hwy turns to ascend, 26 Aug 1981 [all past flower], *Semple 5715,* **2n=36** (MO, NY); Calif Hwy 89, 1.3 km N of Calif Hwy 44 (Old Station), lava flow and gravel road margins, 12 Aug 1990, *Semple et al. 9302* (MO); Hwy 89 N of Lassen Peak, 25 Jul 1972, *Shevock 2215* (RSA). Sierra Co.: ca 5 mi E of La Porte, ca 1/4 mi N of Pacific Mine, yellow pine, 1700 m, 28 Jul 1982, *Ahart 3702* (CAS); Plumas Natl Forest, ca halfway down SE side of Port Wine Ridge to Canyon Creek, 3.1 air km SW of Table Rock, steep, S-facing rock opening in mixed conifer forest, 1603 m, 8 Sep 2008, *Janeway 9578* (JEPS); Sierra Valley, Aug 1874, *Lemmon s.n.* (UC). Siskyou Co.: ca 7.5 mi NE of Weed on Hwy 97, 3700 ft, 2 Jul 1961, *Bacigalupi 7982* (JEPS-2 sheets); Marble Valley, crevices of Marble Rocks, 5500 ft, 8 Aug 1908, *Butler 338* (JEPS, UC); ca 7 mi NNE of Seiad Valley, W of Cook & Green Pass, ca 1/2 air mi from Red Butte, rock crevices, 1850 m, 16 Jul 1986, *Heckard 6324* (JEPS-2 sheets); SE corner of county, 4 Jul 1934, *Howell 12405* (CAS, POM); near Marble Mt. Lookout, dry ridge, 28 Jul 1965, *Muth 311* (RSA); Marble Valley, cracks in marble, 4 Aug 1965, *Muth s.n.* (CAS-2 sheets, RSA); Marble Valley, alpine fell field, 6800 ft, 25 Jul 1966, *Muth 453* (CAS-2 sheets, JEPS); ca 0.1 mi W of Julia Grover Flat, USFS 3, ca 6 air mi W of Mosquito Lake and Whitehorse Flat Reservoir, ca 2 air mi NW of Indian Spring Mtn, yellow pine forest, 3700 ft, 8 Sep 1998, *Oswald & Ahart 9607* (JEPS-2 sheets); Marble Mtn Wilderness Area, Marble Valley Guard Station, 9 Sep 1976, *Stillman 467* (CAS, UCR); Klamath Natl Forest, Hwy 3 ca. 7 mi E of Fort Jones (tributary to Scott River), dry open conifer forest on serpentine, ca. 2000 ft, 30 Jul 1993, *Taylor 14019* (JEPS); SW ridge of Black Mtn, Marble Mtn Wilderness Area, decomposed marble scree, SE-facing slope, 7000 ft, 18 Aug 1963, *Tucker 3753* (RSA); Marble Mtn ridge, limestone, 6750 ft, 12 Aug 2011, *York 3049* (CAS). Tuolumne Co.: Yosemite Natl Park, Jack Main Canyon, 2.4 km SW of Dorothy Lake, marble outcrop, decomposed marble, loamy sand texture, 2717 m, 18 Aug 2005, *Colwell AC05-299* (UC); above NE side of Benson Lake, vernally moist metamorphic bedrock benches in shallow sandy soil, 2460 m, 23 Jul 2003, *Grossenbacher 573* (UC); Yosemite Natl Park, slope above E margin of Benson Lake, base of Piute Mtn, 8650 ft, 11 Aug 1936, *Sharsmith 3813* (DS, UC). **Nevada**. Washoe Co.: Seven Lakes Mtn at N end of Red Rock Valley, with *Artemisia* in a juniper area, 7000 ft, 21 Aug 1985, *Tiehm 10228* (BRY, CAS, COLO, NY, TEX). **Oregon**. Josephine Co.: Illinois River, Anderson Ranch, Siskiyou Forest, shady canyon, rock crevices and among rocks in river bed overflowed during high water but dry and hot during growing season, 1000 ft, 12 Sep 1919, *Ingram 1234* (RM, SOC image); W slope above Illinois River, along trail in Douglas fir-sclerophyll forest, olivine gabbro, 1200 ft, 20 Jul 1951, *Whittaker 537* (WS).

The *Heterotheca villosa* group in the Great Plains

Taxonomic arrangements of the Great Plains heterothecas have varied and identifications have been inconsistent. For the most part, generally recognized entities ("angustifolia," "ballardii," "hispida," "villosa") are tetraploid, which facilitates hybridization and introgression, but ideas of their sympatry and interaction have been obscure and the frequency and abundance of such genetic mixing remains speculative. Diploids occur in *Heterotheca canescens* and *H. stenophylla* and these, too, appear to interact with tetraploids. The treatment here attempts to provide a morphological and evolutionary overview and at least a pragmatic basis for further study.

Harms (1963) included *Heterotheca hirsutissima* (identified as *H. horrida*) as part of this group, but with its consistent diploidy and lack of capitular bracts, it appears to be less immediately related. It does not hybridize or intergrade extensively with any of the "Great Plains villosa group."

Key to Great Plains species of the *Heterotheca villosa* group

1. Leaves linear to narrowly oblanceolate, rigid, margins narrowly revolute; trichome bases strongly multicellular-pustulate.
   2. Involucres 9–17 mm wide (pressed); leaves 1–6 mm wide; leaf and bract margins long-ciliate along at least the proximal 1/2 ..... 15. **Heterotheca stenophylla**
   2. Involucres 5–8 mm wide (pressed); leaves 0.5–2(–4) mm wide; leaf and bract margins eciliate or short-ciliate along proximal 1/5–1/4.
      3. Leaf surfaces short-strigose; phyllaries eglandular and sparsely strigose, or glabrous except minutely glandular proximally, or sparsely sessile-glandular ..... 14. **Heterotheca angustifolia**
      3. Leaf surfaces hispidulous to hispid-hirsute; phyllaries densely sessile-glandular and without other hairs or sessile-glandular and sparsely strigose ..... 16. **Heterotheca scabrifolia**

1. Leaves of various shapes, including linear in *H. canescens*, not rigid, margins not revolute; trichome bases usually wider than the extended portion above but not strongly multicellular-pustulate.
   4. Stems strigose to strigose-sericeous or strigose-villous, hairs antrorsely oriented, sometimes with antrorsely oriented understory and spreading overstory.
      5. Leaf surfaces and phyllary apices eglandular; involucres 11–15 mm wide; rays 20–26 ..... 11. **Heterotheca villosa**
      5. Leaf surfaces and phyllary apices (distal 1/4) sessile-glandular; involucres 7–10 mm wide; rays 12–22 ..... 13. **Heterotheca canescens**
   4. Stems hirsutulous to hirsute, hirsute-pilose to hirsute-villous, or hispid-pilose, hairs spreading to spreading-deflexed in both the understory and overstory.
      6. Stems and leaves densely and conspicuously sessile-glandular; involucres 7–10 mm wide ..... 17. **Heterotheca wisconsinensis**
      6. Stems and leaves eglandular; involucres 8–13 mm wide or (12–)14–20 mm wide.
         7. Heads mostly relatively short-peduncled in a compactly corymboid arrangment; involucres 8–13 mm wide; ray flowers 13–24 ..... 10. **Heterotheca hispida**
         7. Heads mostly long-peduncled and solitary; involucres (12–)14–20 mm wide; ray flowers (25–)30–55 ..... 12. **Heterotheca ballardii**

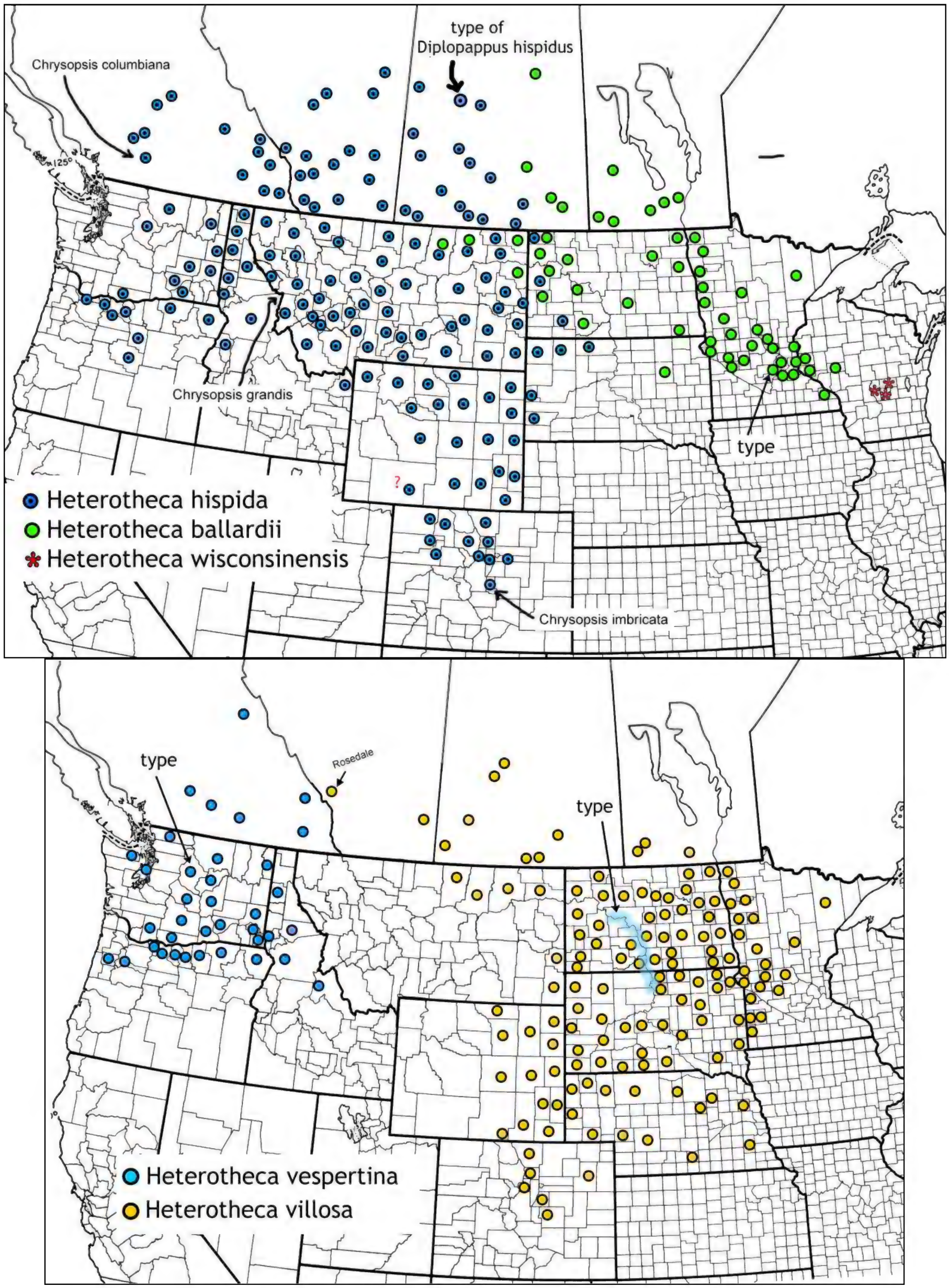


Figure 38. Upper: Distribution of *Heterotheca hispida*, *H. ballardii*, and *H. wisconsinensis*. Lower: Distribution of *H. vespertina* and *H. villosa*. For discussion of the type locality of *H. villosa*, along the stretch of blue-highlighted Missouri River, see Nesom 2020 (Phytoneuron 2020-66: 1–9).

10. HETEROTHECA HISPIDA (Hook.) Nesom, **comb. nov.** *Diplopappus hispidus* Hook., Fl. Bor.-Amer. 2(7): 22. 1834. *Chrysopsis hispida* (Hook.) DC., Prodr. 7: 279. 1838. *Chrysopsis villosa* var. *hispida* (Hook.) A. Gray, Synopt. Fl. N. Amer. 1, 2: 123. 1884. *Heterotheca villosa* var. *hispida* (Hook.) Harms, Brittonia 26: 61. 1974. **TYPE**: **CANADA**. **Saskatchewan**. Carlton House, 1827, *Richardson s.n.* (holotype: BM 1026321 image!).

The BM sheet (upper half, the Richardson collection) includes three separate stems — Semple annotated shoot no. 1 as the "holotype" in 1988 (Fig. 26); he later noted (1990, p. 226) that "The middle shoot No. 1 is designated herein the lectotype" but in 1994 and in 1996 (p. 126) he indicated that "shoot no. 2" (on the left) is the lectotype. All three stems have similar vestiture, leaf shape, and involucre size and all can be construed to be of the same gathering, a single population, thus all are considered here to be part of the type. The stem vestiture is sparsely hirsute-pilose or hispid-pilose, of relatively long, spreading to slightly deflexed hairs in a single story.

Protologue: "totus pilis patentibus hispidus, foliis oblongo-spathulatis basi angustatis subpetiolatis, ramis subcorymbosis, involucri foliolis angustatis acutis glabriusculis. Hab. Carlton-House Fort. *Dr. Richardson*." Semple (1990, p. 226) noted that "Obvious features of the shoot are its glands and relatively few hispid hairs."

Chrysopsis villosa (Pursh) Nutt. var. *discoidea* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 1, 2: 123. 1884. *Diplogon villosum* var. *discoidea* (A. Gray) Kuntze, Rev. Gen. Pl. 1: 334. 1891. **TYPE**: **USA**. **Montana**. [Ravalli Co.]: Cañon from Ross's Hole to Bitterroot Valley, 26 Jul 1880, *S. Watson 141* (holotype: GH image!).

The morphology/vestiture is very similar to that of *Chrysopsis columbiana*. Gray described the heads as "destitute of rays," but as noted by Semple in annotation of the holotype, "rays are present on immature heads, eaten away on mature ones."

Chrysopsis columbiana Greene, Erythea 2: 95. 1894. **TYPE**: **CANADA**. **British Columbia**. protologue: Spencer's Bridge, 1881; label: Spences Bridge, 3 May 1889; *J. Macoun s.n.* (probable holotype: NDG 53892 image!; isotype [as cited by Semple 1990]: CAN).

The NDG specimen does not have an annotation by Greene but it is the only one in his herbarium that closely matches the protologue. The collection date is different and the type locality is Spences Bridge (not "Spencer's," as in the protologue), a long-established community on the Thompson River in south-central British Columbia. Macoun's handwritten label data say "Spences" Bridge, 3 May 1889.

As described by Greene: "Leaves few, scattered, spreading or deflexed: pubescence of both stem and foliage white, spreading and hispidulous." Semple (1990) noted that these plants have a "very dense indument of hairs compared to the type of var. *hispida*." Stems are densely hirsute to hirsute-villous with slightly deflexed hairs in a single story, all medium long, shorter distally.

Chrysopsis imbricata A. Nels., Bot. Gaz. 37: 263. 1904. *Chrysopsis foliosa* var. *imbricata* (A. Nels.) A. Nels. in Coult. & Nels., New Man. Bot. Centr. Rocky Mts., 493. 1909. **TYPE**: **USA**. **Colorado**. [El Paso or Teller Co.]: Pike's Peak, open slopes, 1 Sep 1901, *A. Nelson 8618* (holotype: RM! image!).

The stem vestiture is hirsute-villous with deflexed hairs; leaf surfaces are hirsute-villous. These plants have similarities to *Heterothca pumila* in vestiture, but the heads are in a closely corymboid arrangement and the capitular bracts are linear, at most slightly longer than the involucre.

Chrysopsis grandis Rydb., Bull. Torrey Bot. Club 37: 129. 1910. **TYPE**: **USA**. **Montana**. [Missoula Co.]: Jocko Creek, 1000 m, 16 Jun 1901, *D.T. McDougal 275* (holotype: NY image!).

The morphology/vestiture is very similar to that of *Chrysopsis columbiana* except for slightly larger involucres.

Chrysopsis butleri Rydb., Bull. Torrey Bot. Club 37: 129. 1910. **TYPE**: **USA**. **Montana**. Gallatin Co.: Gateway, 17 Aug 1908, *B.T. Butler 620* (holotype: NY image!).

The stem vestiture is densely and evenly hirsutulous with slightly deflexed hairs in a single story — very similar to that of *Chrysopsis columbiana* but with slightly shorter hairs.

Stems densely hirsutulous to hirsute, hirsute-pilose to hirsute-villous, or hispid-pilose with spreading to spreading-deflexed hairs, usually in a single story but sometimes with an upper story of distinctly longer hairs. Leaf and bract surfaces loosely ascending-strigose to hirsute, margins ciliate. Heads short-peduncled in a corymboid arrangment (sometimes with longer peduncles and toward solitary), usually with narrow but clearly evident capitular bracts. Chromosome numbers, 2n=18, 36.

Semple has made chromosome counts from many populations of *Heterotheca hispida* in Canada (British Columbia, Alberta, Saskatchewan) and in the USA (Oregon, Montana, Wyoming) — diploids occur in each of these states, tetraploids in Alberta, Montana, and Wyoming. I am unable to find a morphological or geographical pattern to the occurrence of the tetraploids, but variation in the species (as recognized here) is complex and it seems likely that further study of chromosome numbers could be helpful toward a better understanding of evolutionary patterns.

Stem vestiture of *Heterotheca hispida* is consistently spreading but variable in length and density. Particularly in Montana, stems are densely hirsutulous (exemplified by the type of *Chrysopsis butleri*; also Fig. 40) with stiff, sharp-pointed, distinctly deflexed hairs. Variants in Montana and elsewhere, especially in Canada, have less dense vestiture of longer hairs; the type of *Diplopappus hispidus* is an extreme example of this (Fig. 39), with vestiture suggestive of *H. hirsuta* but lacking the glandularity of the latter. As interpreted here, the geographic coherence of this variable system of plants suggests that a single entity is represented (with at least one significant caveat, as in the following paragraph).

In Carbon Co., Wyoming, and adjacent areas of the Albany, Fremont, and Natrona counties (the Platte/Laramie River Drainage area), there appears to be a "race" within what is identified here as *Heterotheca hispida* of relatively small-statured plants with mostly 1-headed stems, short, spreading stem vestiture, and evident sessile-glandular leaf surfaces seen through the non-glandular hairs. These plants were abundantly collected by Univ. of Wyoming student Amy Roderick in 1997 and 1998. It does not appear to be an early-season growth form, as collections have been made through early September. More characteristic *H. hispida* occurs in the same area but not as abundantly. A plausible speculation is that this population system originated as a hybrid between *H. hispida* and *H. hirsuta*, which are sympatric in the area. Plants of similar aspect occur sporadically elsewhere (in the RM collections, they are common in Park Co., Wyoming), but they lack the distinctive glandularity of those in the Platte/Laramie area. The type of *Chrysopsis mollis* Nutt. (see *H. villosa* synonymy) may be a plant of this population system — it was collected by Nuttall apparently in close proximity to the type of *C. foliosa* Nutt., which is identified here as *H. villosa*. Field study may be able to provide a more definitive perspective.

Representative records examined for *Heterotheca hispida* in South Dakota. Corson Co.: 5 mi NW of Wakpala, prairie hilltop pasture, 12 Sep 1968, *Stephens 29166* (> *H. villosa*?; KANU image!). Lawrence Co.: Spearfish, Lookout Mtn Park, at the end of Pony Express Lane, ridge line, 1358 m, 1 Sep 2013, *Halse 8954* (BRY, CAS). Perkins Co.: 1 mi S, 10 mi E of Bison, upland shortgrass prairie, 26 Jul 1966, *Stephens 8000* (KANU image!).

Records examined for North Dakota. Divide Co.: *Harms 18512* (KANU image!). Hettinger Co.: *Stephens 50083* (KANU image!). McKenzie Co.: Little Missouri National Grassland, 6 mi S, 2 mi W of Cartwright, NW-facing prairie slope, 24 Jul 1981, *Rohde 3051* (MO).

Utah: Salt Lake City, Aug 1879, *M.E. Jones s.n.* (POM) – the ID is unambiguous but the collection was far out of range, possibly a waif, more likely an aberrant form of *Heterotheca utahensis*. Not mapped as *H. hispida*.

Figure 39. *Heterotheca hispida*. Upper: BM holotype of *Diplopappus hispidus*. Lower: Details from middle stem of holotype.

Figure 40. *Heterotheca hispida*, common and abundant expression. Bozeman, Montana. Photo by Matt Lavin, 27 June 2003.

Figure 41. *Heterotheca hispida*. Representative collection, Sheridan Co., Montana, *Stephens 13194* (KANU).

11. HETEROTHECA VILLOSA (Pursh) Shinners, Field & Lab. 19: 71. 1951. *Amellus villosus* Pursh, Fl. Amer. Sept. 2: 564. 1814 [1813]. *Inula villosa* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 151. 1818. *Diplopappus villosus* (Pursh) Hook., Fl. Bor.-Amer. 2: 22. 1834. *Chrysopsis villosa* (Pursh) Nutt. ex DC., Prodr. 5: 327. 1836. *Diplogon villosum* (Pursh) Kuntze , Revis. Gen. Pl. 1: 334. 1891. **TYPE**: [**South Dakota** or **North Dakota**]. Protologue: "On the Missouri," June or early July, *J. Bradbury s.n.* (holotype: apparently lost or destroyed, fide Semple 1990). **NEOTYPE** (Nesom 2019, p. 4): Label: "Missouri, Nuttall." As deduced: Along the Missouri River in South Dakota or North Dakota, July or August 1811, *T. Nuttall s.n.* (PH-001726/00002717, stem no. 2, image!). **Superceded neotype** (Semple 1990, p. 225): ["UNITED STATES. Missouri, [in 1811], *Nuttall s.n.* (PH-001726, shoot no. 1, image!)." Locality as deduced (see Nesom 2019): Along the Missouri River in South Dakota or North Dakota, July or August, 1811.

Heterotheca foliosa (Nutt.) Shinners, Field & Lab. 29: 71. 1951. *Chrysopsis foliosa* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 316. 1841. *Chrysopsis villosa* var. *foliosa* (Nutt.) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca villosa* var. *foliosa* (Nutt.) Harms, Wrightia 4: 15. 1968. **TYPE**: [**Wyoming**. Probably Natrona Co.]: Protologue: "In the Rocky Mountain plains, near the banks of the Platte. Flowering in August," [early Jun 1834], *T. Nuttall s.n.* (holotype: BM image!, 3 stems, probably from 2 or 3 different plants, but reasonably from the same population; isotype: GH 55855 image!, stem on right side of sheet).

The BM collection has Nuttall's annotation as "Chrysopsis * foliosa, R. Mts." The right-hand stem of GH 55855 is essentially identical in morphology to those on the BM sheet; the label in Nuttall's script says "Chrysopsis foliosa Nutt., E side of Rocky Mts." The left-hand plant (GH 5585) has spreading reflexed stem vestiture and is identified here as *Heterotheca hispida*.

Nuttall, with Wyeth's expedition, traveled along the North Platte River in central Wyoming in early June (ca. 6-12 June) 1834, probably in Natrona County (see Wyeth 1834). If the collection of *Chrysopsis foliosa* were made in June, the nature of his reference to "Flowering in August" is not clear (the Wyeth expedition was already west of Fort Hall, Idaho, by August), but perhaps he observed that full flowering of the population would be reached by that month (the stems of the holotype are in full flower). Nuttall's description of *C. foliosa*, especially features of the leaves, puts it close to the present concept of *H. villosa*: "About foot high, sending up many hairy stems from the same root. Nearly allied to *C. villosa* but far more pubescent and hoary, with the leaves widest at the base ... sericeously villous, and more or less canescent ... flowers fastigiate, corymbose; leaves entire, oblong or oblong-ovate, subamplexicaule .... A very showy species." Neither overstory nor understory is clearly antrorsely appressed, however, but rather all stem vestiture of Nuttall's collection is spreading with a slight but distinct antrorse orientation — these plants perhaps are introgressants between *H. villosa* and *H. hispida*.

Chrysopsis mollis Nutt., Trans. Philos. Soc. n.s., 7: 316. 1841. **TYPE**: [**Wyoming**. Probably Natrona Co.]: Protologue: "In the Rocky Mountain plains, near the banks of the Platte, [early Jun 1834]." Label: "R. Mts." *T. Nuttall s.n.* (holotype: BM image!; isotype: PH 25429 image!).

Labels on both the BM and PH specimens have "Chrysopsis * mollis" handwritten by Nuttall.

Heterotheca villosa in the strict sense is characterized by heads in a closely corymboid capitulescence, involucres 11–15 mm wide and subtended by capitular bracts, and loosely strigose-villous leaves and stems with eglandular surfaces. Stem vestiture is 2-storied — the understory is antrorsely oriented while the overstory comprises much longer, spreading hairs. Chromosome number, $2n$=36 (Semple 2008).

Figure 42. *Heterotheca villosa*, Lawrence Co., South Dakota. *Stephens 16844* (KANU).

Figure 43. *Heterotheca villosa*, Harding Co., South Dakota. *Stephens 7929* (KANU). On proximal half of stem, all hairs spreading; on distal third, understory antrorse with spreading overstory.

Figure 44. *Heterotheca villosa*, Butte Co., South Dakota. *Stephens 24506* (KANU). Numerous lateral branches have arisen below damage to the primary axis. Strigose vestiture of relatively short, coarse hairs and stiffly spreading marginal cilia suggest an influence from *H. angustifolia*.

The types of *Chrysopsis mollis* and *C. foliosa* were apparently collected by Nuttall at the same locality and were described simultaneously (in sequence, both on page 316). For *C. mollis*, he noted "HAB. With the above, which it much resembles, but the leaves are more oblong, not in the least scabrous nor any where ciliate; the stem, also, softly villous." The capitular bracts of *C. mollis* are nearly filiform and give the plant a distinct appearance, which obviously Nuttall saw, but there is no other species besides *H. villosa* in this region with close, densely strigose-villous stem vestiture and 'softly villous' leaf vestiture — *C. mollis* is interpreted here to be a variant of *C. villosa*, possibly genetically influenced by some other species, perhaps even a distinct but previously unrecognized species (see further comments under *H. hispida* regarding a population system in Albany, Carbon, Fremont, and Natrona counties, Wyoming).

Where *Heterotheca villosa* and *H. hispida* occur in sympatry — a relatively small part of the geographic range of each species (e.g., in eastern Wyoming and adjacent areas) — putative intermediates are commonly encountered but most plants can usually be placed in one or the other species, indicating that gene flow is occurring but that some degree of isolation is in effect. This taxonomy can be seen as somewhat arbitrary but it serves a pragmatic purpose and if the evolutionary interpretation is correct, it also reflects the biological situation of two distinct entities with hybridization and introgression in their area of sympatry. The taxonomic distinction is essentially based on orientation of stem vestiture — spreading to slightly deflexed in *H. hispida* vs. at least the understory distinctly antrorse in *H. villosa*. As noted above, the type of *Chrysopsis foliosa* perhaps is an introgressant; it seems to be a morphological intermediate.

The situation between *Heterotheca villosa* and *H. ballardii* is similar, although *H. ballardii* (vs. *H. hispida*) is sympatric over a greater part of its total range with *H. villosa*. Both taxa apparently are at least primarily tetraploid where sympatric and putative intermediates or introgressants are frequently encountered but the distinction between *H. villosa* and *H. ballardii* in typical form is more pronounced than between *H. villosa* and *H. hispida*. *Heterotheca ballardii* (compared to *H. villosa*) has longer peduncles and spreading stem vestiture in understory and overstory (see Nesom 2020 for further discussion and comparison).

Westernmost record. **Montana**. Blaine Co.: 0.25 mi W of Ft. Belknap, brushy, weedy floodplain of Milk River, dry sandy soil, 20 Jul 1973, 20 Jul 1973, *Stephens 68271* (KANU image!).

12. HETEROTHECA BALLARDII (Rydb.) Nesom, **comb. nov.** *Chrysopsis ballardii* Rydb., Brittonia 1: 100. 1931. *Heterotheca villosa* var. *ballardii* (Rydb.) Semple, Novon 4: 53. 1994. **TYPE**: **Minnesota**. [Carver Co.]: Chaska, Jul 1891, *C.A. Ballard 640* (holotype: MIN image!).

Heterotheca ballardii is characterized by its relatively large heads solitary or loosely clustered on long peduncles, the heads with narrow, coarsely ciliate capitular or subcapitular bracts. Stems hirsute with spreading to slightly deflexed hairs, sometimes loosely antrorsely oriented (influence of *H. villosa* ?); leaves oblong to oblanceolate, epetiolate, not clasping; stems, leaves, and phyllaries eglandular; involucres (12–)14–20 mm wide (pressed); ray flowers (25–)30–55. See Nesom (2020) for photos of the type and representative specimens. Chromosome number, $2n$=36 (Semple 2008).

The concept here of *Heterotheca ballardii* is generally similar to Semple's (as *H. villosa* var. *ballardii*). He noted (1994, p. 53) that it "is the generally robust, larger-headed, many-rayed, eglandular, oblong-leaved race of the species occurring on the northeastern prairies of Canada and the United States. Typical variety *villosa* has oblanceolate leaves and smaller heads with fewer rays."

Figure 45. *Chrysopsis ballardii*, Carver Co., Minnesota. Holotype (MIN).

Heterotheca ballardii is sympatric over nearly its entire range with *H. villosa* — intermediates are encountered but each can be recognized in fairly typical form. *Heterotheca ballardii* and *H. hispida* slightly overlap in range but I have not seen obvious morphological intermediates between them — *H. hispida*-like plants (with a more congested inflorescence, especially) are scattered through the range of *H. ballardii* but this probably is parallelism or genetic influence of *H. villosa*.

Collections of each of the three species noted above have been made in McKenzie County in western North Dakota:

Heterotheca ballardii. 5 mi N, 10 mi E of Watford City, roadside ditch, 8 Jul 1980, *Rohde 1338* (MO).

Heterotheca hispida. 6 mi S, 2 mi W of Cartwright, Little Missouri Natl Grassland, NW-facing prairie slope, 24 Jul 1981, *Rohde 3051* (MO).

Heterotheca villosa. 14 mi S, 3 mi W of Watford City, North Unit, Theodore Roosevelt Natl Park, Squaw Creek Campground, road edge, 9 Jul 1980, *Rohde 1370* (MO).

Montana records (representative) for *Heterotheca ballardii*. Richland Co.: 19 mi N of Sidney, upland prairie pasture hillside, 28 Jun 1968, *Stephens & Brooks 23581* (KANU image!). Sheridan Co.: 4 mi W of Westby, upland prairie pasture, 5 Jul 1967, *Stephens & Brooks 13194* (KANU image!). In Valley and Phillips counties, many collections of *H. ballardii* were made by J.M. Charboneau in 2010 and 2011 (all at RM) — in these counties, typical *H. ballardii*, typical *H. hispida*, and intermediates occur.

13. HETEROTHECA CANESCENS (DC.) Shinners, Field & Lab. 19: 68. 1951. *Haplopappus canescens* DC., Prodr. 5: 349. 1836. *Chrysopsis canescens* (DC.) Torr. & A. Gray Fl. N. Amer. 2(2): 256. 1842 [nom. illeg.], not *Chrysopsis canescens* DC., Prodr. 5: 328. 1836. *Chrysopsis villosa* var. *canescens* (DC.) A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. *Chrysopsis berlandieri* Greene [nom. nov.], Erythea 2: 96. 1894. **TYPE: Texas**. Protologue: "4 in Mexicanae prov. Texas districtibus orientalibus nov. et dec. flor. legit cl. Berlandier (pl. exs. n. 1877)" — GH label: "Comancheries orientales des Texas, Nov. et Dec. 1828," No. 502 [ex 10] = 1877 (holotype: G-DC; isotypes: GH, HAL, NY, US, WIS). Images! of all types.

The trip made by Berlandier in November and December 1828 began in San Antonio (Bexar Co.) and looped through Kendall, Kerr, Bandera, Uvalde, and Medina counties (see Figure 46). *Heterotheca canescens* is known from each of these counties except Medina.

Flowering May–Aug(–Sep). Sandy clay, clay loam, black clay, limestone and igneous soils, sandy gypseous soils, rocky and gravelly soils, sandstone outcrops, dunes, prairies, open hills, alluvium, roadsides, fencerows; 100–2600 ft.

Heterotheca canescens is characterized by "(1) the dense canescent, sericeous pubescence of its phyllaries, leaves, and stems, (2) small, short-rayed heads, (3) narrow, upper and middle leaves and deciduous lower leaves, (4) numerous sivery-canescent axillary shoots, and (5) a highly rhizomatous habit" (Harms 1963, p. 30). The vestiture is densely strigose and silvery gray-green but plants of some collections may dry with a darker color and "there is usually some variation in the degree of canescence in larger colonies, with separate clones frequently distinguishable by slight differences in color aspect" (Harms, p. 37). Leaf surfaces are prominently sessile-glandular beneath the strigose vestiture. Its characterization as "rhizomatous" alludes to the production of caudex branches or offsets that become long and node-rooting like rhizomes — these are not a consistent feature in herbarium specimens, but in the field, *H. canescens* usually shows a distinctly colonial aspect.

The description of *Heterotheca canescens* by Harms referred only to diploid populations, but it essentially characterizes tetraploids as well (see Fig. 32 and coFmments below). He noted (p. 35) that the species represents a consistently diploid and "rather uniform species ... stretched along a

relatively narrow corridor" from southern Texas north to central Kansas and that (p. 37) "The primary taxonomic problem involving *H. canescens* results from the close approach to it of various segregants of the Texas populations of *H. villosa* [referring to *H. angustifolia*, as identified here]."

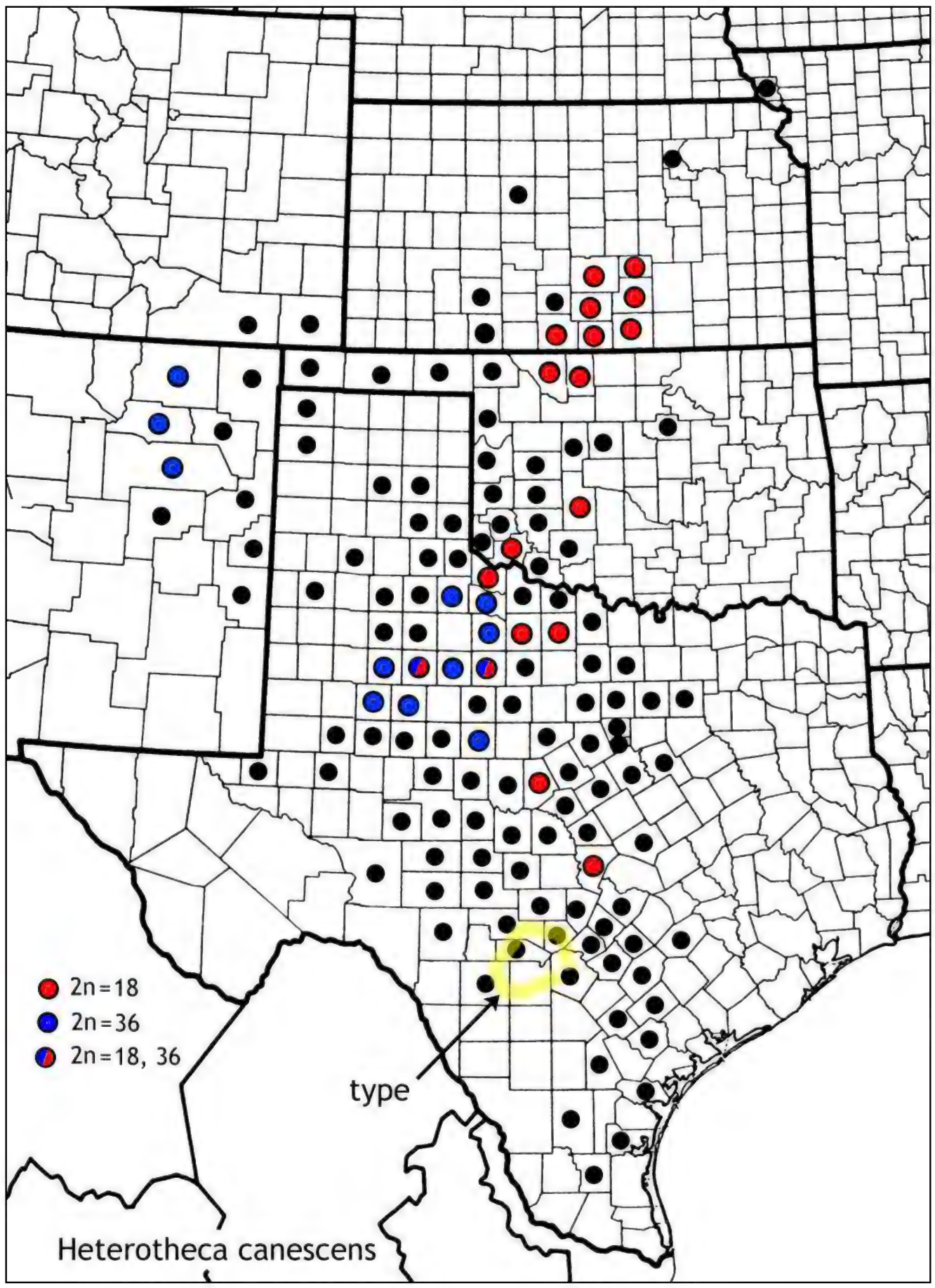


Figure 46. Distribution of *Heterotheca canescens*. Chromosome numbers mapped mostly from data of Harms and Semple. Yellow highlight outlines the route of Berlandier's 1828 trip (see note under type summary, above) — the type collection was made somewhere along his route.

Harms (1963) identified all tetraploid *Heterotheca* in New Mexico and northwestern Texas as part of *Heterotheca villosa* var. *angustifolia*, but differences in vestiture and habit distinguish *H. canescens* (key couplet below). In some places, the two species are distinct in close proximity (e.g., Fig. 56, Crosby Co., Texas); intermediates occur through their area of sympatry, where both are tetraploid (Figs. 57 and 58). New Mexico plants of *H. canescens* outside of the range of *H. angustifolia* (west of it, in Colfax, San Miguel, and Mora counties) and apparently without its genetic

influence, have a colonial habit and silvery, silky-sericeous vestiture. Similar plants are found in other New Mexico counties, where typical *H. angustifolia* also occurs.

In the range of diploid (typical) *Heterotheca canescens*, leaves are mostly linear to linear-oblanceolate, and Harms (1963) identified only these plants as *H. canescens*. In its tetraploid range, *H. canescens* (including colonial forms with sericeous vestiture) produces more distinctly oblanceolate leaves, more like *H. angustifolia*. Correlation between ploidy level and leaf shape in *H. canescens* seems strong enough that taxonomic recognition of two entities might be justified.

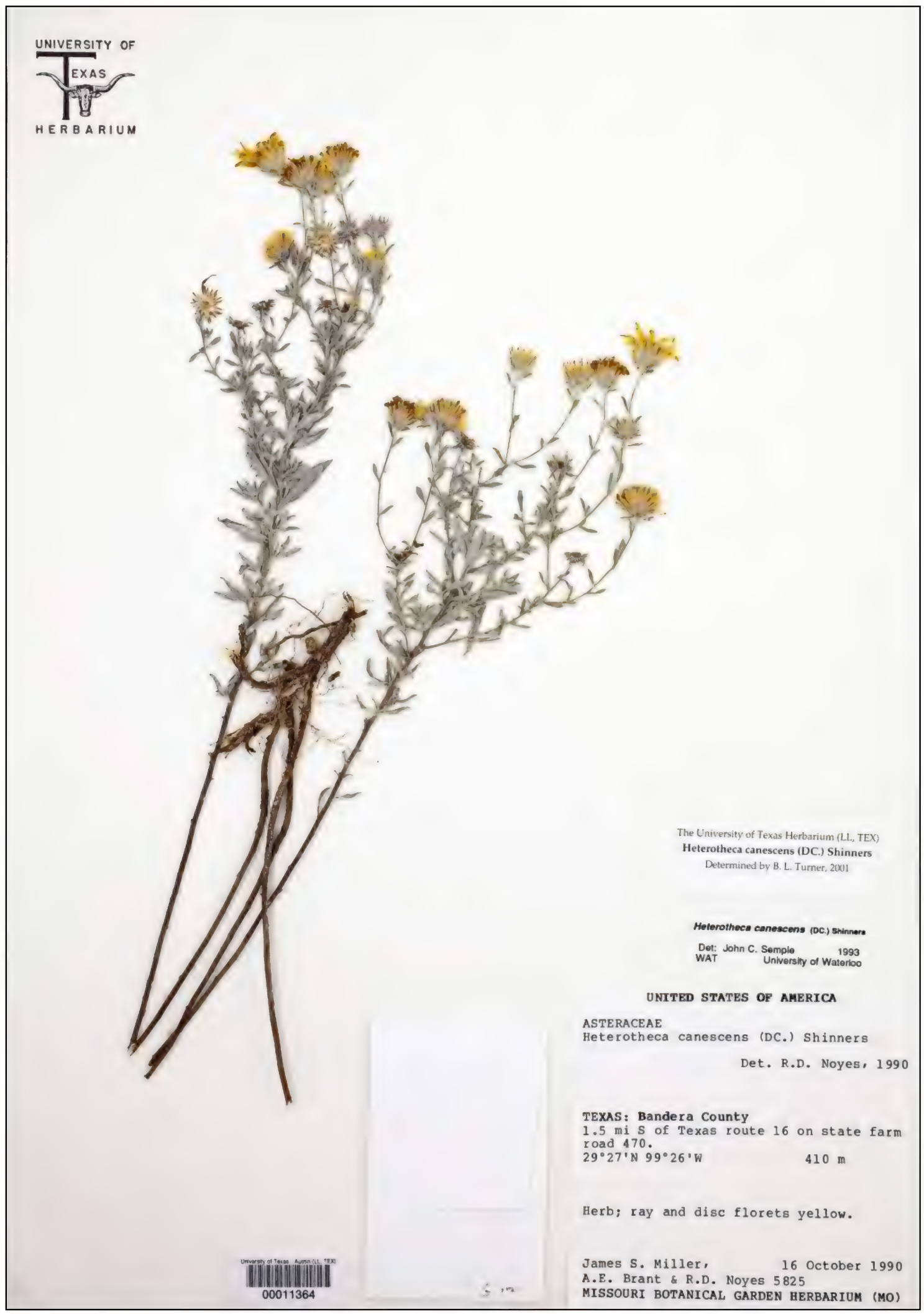


Figure 47. *Heterotheca canescens*, Bandera Co., Texas, area of type locality. *Miller 5825* (TEX).

Figure 48. *Heterotheca canescens*, Uvalde Co., Texas, area of type locality. *Correll & Johnston 18135* (LL).

Figure 49. *Heterotheca canescens*, San Saba Co., Texas. Strongly colonial habit. *Burleson 593* (BRIT).

Figure 50. *Heterotheca canescens*, Colfax Co., New Mexico. *Harms 19113* (KANU). The northwestern, tetraploid population system (see map in Fig. 46) tends to have vestiture less dense than typical and relatively broad leaves.

Figure 51. *Heterotheca canescens*, Union Co., New Mexico. *Harms 19110* (KANU). Perhaps influenced by *H. angustifolia*. Leaves are silvery-sericeous but narrower than in the plant in Figure 50.

Figure 52. *Heterotheca canescens*, probably with influence of *H. angustifolia*, Lamb Co., Texas. *Turner & Melchert 4828* (TEX).

Plants of *Heterotheca canescens* from Holt Co., Missouri (Mound City, on the mounds, 29 Sep 1931, *Kellogg s.n.*, MO), apparently are disjunct and represent the northernmost extension of the species — they perhaps are influenced by genes of *H. angustifolia*.

Plants from trans-Pecos Texas with a vestiture similar to *Heterotheca canescens* (closely strigose, silvery-sericeous), identified by Harms (1963) as "the Davis Mt. variant" and by Semple (2006) as disjunct populations of *H. canescens*, are identified here as *H. zionensis* at the southeastern end of it range. Plants of *H. zionensis* produce stems thicker, taller, more sparingly branched, more sparsely leafy and without prominent axillary tufts of small leaves, they are more erect from the base, strictly caespitose, without rhizomes, and the heads lack capitular bracts.

The ranges of *Heterotheca pedunculata* and *H. canescens* appear to be contiguous or nearly so in north-central New Mexico, but the two apparently do not intergrade. Both have relatively dense and closely strigose vestiture of thin-based hairs, but *H. canescens* has longer, thicker, and more densely leafy stems, axillary buds and axillary tufts of leaves, prominent marginal leaf cilia, and larger heads with narrower phyllaries. *Legler 10441* and *10813* from Vermejo Park Ranch in Colfax County are *H. canescens*; *Legler 10327* (COLO image!, RM, UNM image!) is *H. pedunculata*.

14. HETEROTHECA ANGUSTIFOLIA (Rydb.) Nesom, **comb. nov.** *Chrysopsis angustifolia* Rydb., Bull. Torrey Bot. Club 37: 128. 1910. *Heterotheca villosa* var. *angustifolia* (Rydb.) Harms, Wrightia 4: 16. 1968. *Chrysopsis villosa* var. *angustifolia* (Rydb.) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca stenophylla* var. *angustifolia* (Rydb.) Semple, Novon 4: 53. 1994. **LECTOTYPE** (Semple 1990): **Nebraska**. Hooker Co.: Near Mullen, Middle Loup River, on sandhills, 14 Sep 1893, *P.A. Rydberg 1766* (NY; isolectotypes: GH, NEB [typo as *Rydberg* "*1716*"], NY, US). Images! of all types.

Perennial, caespitose from a thick, woody taproot, without rhizomes. Vestiture of leaves and stems loosely strigose with stiff, thick-based hairs not obscuring the green surfaces. Leaves rigid, oblanceolate to narrowly oblanceolate, ascending, margins narrowly revolute. Heads mostly short-pedunculate in a closely clustered capitulescence, with closely subtending linear to linear-lanceolate capitular bracts; involucres 5–8 mm wide.

Heterotheca angustifolia has been treated as a variety of *H. stenophylla* (by Semple) and a variety of *H. villosa* (by Harms), and it might also plausibly be taxonomically linked with *H. canescens*, in view of their intergradation (analogous to that between *H. angustifolia* and *H. villosa*). It is consistently tetraploid (2n=36, many counts) and apparently hybridizes and intergrades with *H. villosa* and with *H. canescens* in areas of sympatry. On the other hand, *H. angustifolia* in its characteristic (typical) form occurs throughout its range, from South Dakota to Texas, and it is reasonably regarded as a distinct species. Intemediates with *H. stenophylla* are encountered rarely.

a1. Leaves rigid, margins narrowly revolute; trichomes rigid with pustulate bases; involucres 5–8 mm wide ..... 14. **Heterotheca angustifolia**

a1. Leaves not rigid, margins flat; trichomes usually loose with bases usually wider than the extended portion above but not strongly pustulate-based; involucres 11–15 mm wide ..... 11. **Heterotheca villosa**

a2. Leaves oblanceolate, rigid, margins narrowly revolute; axillary tufts of small leaves absent or not dense and prominent; vestiture sparse to moderately dense and not obscuring the green epidermis, trichome bases strongly pustulate; leaf surfaces and phyllary apices eglandular; plants caespitose, not rhizomatous ..... 14. **Heterotheca angustifolia**

a2. Leaves linear to narrowly oblanceolate, not rigid, margins flat; axillary tufts of small leaves abundant and prominent; vestiture dense and silvery-sericeous, trichome bases usually wider than the extended portion above but not strongly pustulate; leaf surfaces and phyllary apices sessile-glandular; plants colonial, rhizomatous ..... 13. **Heterotheca canescens**

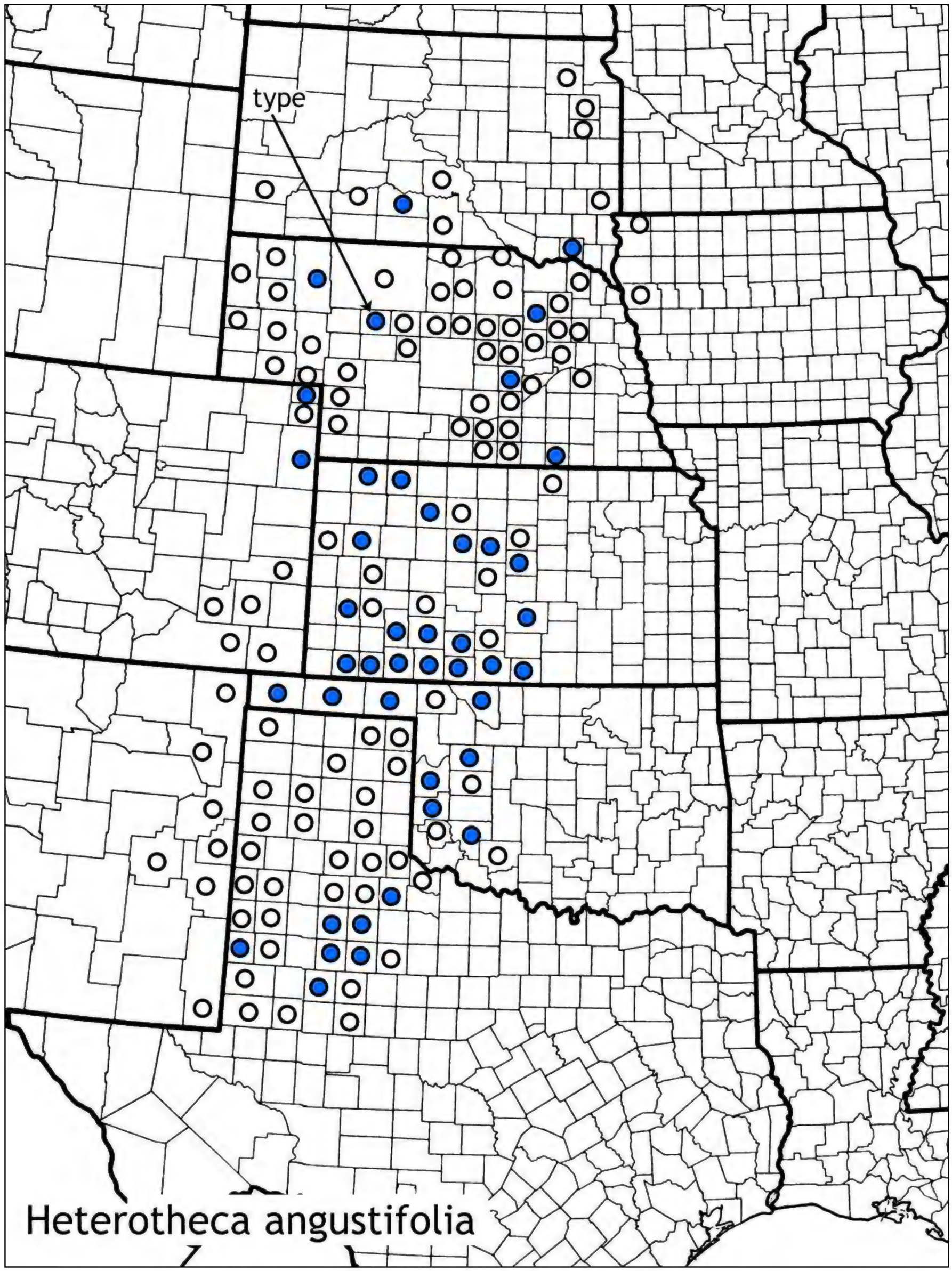


Figure 53. Distribution of *Heterotheca angustifolia*. Blue symbols are tetraploid chromosome counts, data mostly from Harms and Semple.

Figure 54. Typical *Heterotheca angustifolia*, Rawlins Co., Kansas, where sympatric with neither *H. villosa* nor *H. canescens*. *Harms 1255* (KANU).

Figure 55. *Heterotheca angustifolia*, typical form, Hemphill Co., Texas. *Rowell 4071* (TEX).

Figure 56. *Heterotheca* from Crosby Co., Texas, apparently representing a mixed collection of two sympatric species — *H. angustifolia* (dark green) and *H. canescens* (silver-gray). *Tharp 4536* (TEX).

Figure 57. *Heterotheca angustifolia*, Texas Co., Oklahoma. *Harms 1974-B* (KANU). Nearly typical morphology and vestiture, although annotated by Harms as possibly intermediate with *H. canescens*. See Fig. 58 from Texas County.

Figure 58. *Heterotheca angustifolia*, Texas Co., Oklahoma. *Harms 1974* (KANU). Vestiture of this plant, with thin-based hairs, is more like *H. canescens*.

The ranges of *Heterotheca pedunculata* and *H. canescens* appear to be contiguous or nearly so in north-central New Mexico, but the two apparently do not intergrade. Both have relatively dense and closely strigose vestiture of thin-based hairs, but *H. canescens* has longer, thicker, and more densely leafy stems, axillary buds and axillary tufts of leaves, prominent marginal leaf cilia, and larger heads with narrower phyllaries. *Legler 10441* and *10813* from Vermejo Park Ranch in Colfax County are *H. canescens*; *Legler 10327* (COLO image!, RM, UNM image!) is *H. pedunculata*.

15. HETEROTHECA STENOPHYLLA (A. Gray) Shinners, Field & Lab. 19: 68. 1951. *Chrysopsis hispida* var. *stenophylla* A. Gray, Boston J. Nat. Hist. 6 (Pl. Lindh.): 223. 1850. *Chrysopsis villosa* var. *stenophylla* (A. Gray) A. Gray, Synopt. Fl. N. Amer. (ed. 2) 1(2): 123. 1884. *Chrysopsis stenophylla* (A. Gray) Greene, Erythea 2: 96. 1894. **TYPE**: **Texas**. [Llano Co.]: Protologue: "On the Llano, from strong ligneous roots in crevices of smooth granite rocks, Nov," 1847, *F.J. Lindheimer 631* (holotype: GH 55862 image!; isotypes: BRIT!, CAN, DS image!, GH 55861 image!, K, MO!, ND-G, NY-4 sheets images!, P-2 sheets images!, US image!, YU image!).

Heterotheca stenophylla occurs on granite and limestone in the Edwards Plateau of central Texas (the type from a granite habitat) — it is characterized by large, solitary heads and rigid, linear to narrowly oblanceolate leaves and capitular bracts with narrowly revolute, long-ciliate margins. The hispid trichomes have distinctly pustulate bases. Leaves and bracts sometimes are glandular. Ray flowers 12–27. Chromosome number, $2n$=18 (Burnet Co.: *R. Johnson 1907-a*, KANU; *McGregor 16792*, KANU; both vouchers were cited by Harms 1974 and Semple 2008, but they are not in the KANU database; *Semple 2198*, as cited below).

Flowering (Apr–)Jun–Oct(–Nov). Cracks, crevices, and ledges and shallow soil pockets in granite and limestone; 900-1900 m. The species in the concept here is endemic to the Edwards Plateau of central Texas.

Heterotheca stenophylla, regarded here as an uncommon Edwards Plateau endemic, differs in morphology, geography, and ecology from plants previously identified as typical *H. stenophylla* from prairie habitats further north and northwest in Texas and from Oklahoma to Nebraska. The prairie population system is identified here as *Heterotheca scabrifolia*. The diploid chromosome count for typical (large-headed) *H. stenophylla* suggests that the size difference in heads between species cannot be attributed to a ploidal difference.

1. Heads 9–17 mm wide (pressed), solitary at ends of long branches or loosely clustered on leafy-bracteate peduncles 2–7 cm long; leaves 1–6 mm wide, leaf and bract margins long-ciliate usually along at least the proximal 1/2; phyllaries eglandular and sparsely strigose, glabrous or sometimes minutely glandular proximally, or sparsely sessile-glandular ..... 15. **Heterotheca stenophylla**

1. Heads 5–8 mm wide (pressed), usually in cymiform to subcymiform clusters on leafy-bracteate peduncles (0.5–)1–2.5 cm long, rarely solitary; leaves 0.5–2(–4) mm wide, leaf and bract margins eciliate or short-ciliate along proximal 1/5–1/4; phyllaries densely sessile-glandular and without other hairs or sessile-glandular and sparsely strigose ..... 16. **Heterotheca scabrifolia**

Additional collections, typical *Heterotheca stenophylla*. Texas. Burnet Co.: Inks Lake State Park, ca. 0.5 mi SE of SE end of Inks Dam, ca. 960 ft, occasional, with two *Cheilanthes* spp., rooted in fractures of dry boulders of Valley Spring Gneiss exposed on sparsely vegetated hills along powerlines, 13 Jun 1995, *Carr 14692* (TEX); 1.8 mi S of Inks Park Headqtrs, crest of hill just S of park on P-4, a few scattered plants growing among rocks, 18 Jun 1976, *Semple 2198* (BRIT, TEX). Hays Co.: Wimberly, 22 Jul 1946, *Correll 13398* (BRIT); 7 mi. ENE of jct with Co. Road 32 in Fischer (Comal Co.) on county road toward Woodcreek, at crossing of Blanco river in west-central part of Hays Co., area of oak woods in rolling hills, on steep, rocky bank along river, branches

somewhat pendent, 13 Oct 1990, *Nesom 7230* (TEX, UTEP); ca. 0.75 mi NNW of Wimberley, near jct of Cypress Creek and Blanco River, 9 Aug 1961, *Walker 8* (BRIT, TEX). Kimble Co.: Exit ramp to Hwy 290 from IH-10, road to Fredericksburg, S side of Hwy 290, 13 Jun 1999, *Turner 99-378* (TEX). Llano Co.: Llano, arid rocks, 15 May 1899, *Bray 331* (TEX); near summit of Turkey Peak just east of Enchanted Rock, locally abundant in crevices of granitic boulders, 24 Jul 1976, *Butterwick 2996* (TEX); S bank of Llano River ca. 15-50 ft E of State Hwy 16 bridge in Llano, locally common on granite boulders on unshaded steep slope, 7 Jun 1988, *Carr 8932* (BRIT); 7.5 mi E of Llano on Texas 29, granite rock deposits, 1 Jul 1983, *Keeney 3555* (BRIT); between Llano and San Saba, along Hwy 16, on upper slopes of granite ridge, 29 Apr 1946, *Lundell 14576* (LL); Llano, 11 Jun 1930, *Tharp 7356* (LL). McCulloch Co.: S of Brady, along Hwy 87, 7.2 mi S of jct with Hwy 71, roadside park along the banks of the San Saba River, low stony hill range site, limestone ledge immediately above the river, 28 Aug 2013, *Hansen 7562* (TEX). Mason Co.: SW of Mason along Farm Road 1871, 9.1 mi SW of junction with Hwy 87, at Llano River crossing, loamy bottomland range site, limestone ledge above the river, 12 Sep 2013, *Hansen 7683* (TEX); Mason Mt. Wildlife Management Area, 5 air mi NNW of Mason, 2.1 mi N of jct of Hwy 29 and Hwy 398 then 2.4 mi NW on dirt road, 24 Sep 1999, *Singhurst et al. 8203* (TEX); W of Mason, among granite rocks, 23 Jul 1946, *Wolff s.n.* (TEX). Menard Co.: NE of Hext, near the San Saba River crossing along Ranch Rd 1311, 3.15 mi N of its jct with Texas Hwy 29, roadside, 8 Jul 1989, *Lievens 4095* (LSU). Travis Co.: Streambed crossing between Hamilton Pool turnoff and Pedernales River on Hamilton Pool road (FM 3238), shallow soil pockets on bare limestone, bordered by *Platanus*, *Fraxinus*, etc., in oak and cedar woodland, ca. 900 ft, 18 Sep 1983, *Ertter 5146* (TEX); on boulder of Hamilton Creek, below Hamilton Pool, one population found on one large boulder, 1 Nov 1979, *Johnston s.n.* (TEX).

16. HETEROTHECA SCABRIFOLIA (A. Nels.) Nesom, **comb. nov.** *Chrysopsis scabrifolia* A. Nels., Bot. Gaz. 37: 264. 1904. **TYPE**: **Oklahoma**. Woods Co.: [no other locality data,] 29 Jun 1900, *P.J. White s.n.* (holotype: RM! digital image!).

Heterotheca scabrifolia previously has been identified as *H. stenophylla* (as *H. stenophylla* var. *stenophylla* by Semple), with which it shares rigid, linear to narrowly oblanceolate leaves, capitular bracts with revolute, ciliate margins, and vestiture not obscuring surfaces, the trichomes with distinctly multicellular-pustulate bases — but *H. scabrifolia* is distinct in its relatively small, distally clustered heads, more consistently glandular herbage, and shorter marginal cilia (see key couplet, p. 72). Ray flowers 14–20. Chromosome numbers, 2*n*=18, 36.

Flowering Jun-Oct. Plains and open hills, sandstone outcrops, dunes and sandhill prairies, gypsum outcrops and hills, red, gravelly soil, gypsiferous sandy loam, calcareous roadbanks, creek terraces; 1500–2700 ft.

Differences in head size and arrangement between *Heterotheca scabrifolia* and *H. stenophylla* are consistent. Plants from Taylor Co. and Eastland Co., Texas (Figs. 73 and 74; mapped in Fig. 59), slightly north of the range of *H. stenophylla*, have small, clustered heads characteristic of *H. scabrifolia* but the densely long-ciliate leaf and bract margins of typical *H. stenophylla*, not seen elsewhere in *H. scabrifolia*. These are the only collections observed that suggest incomplete differentiation or some past episode of gene flow.

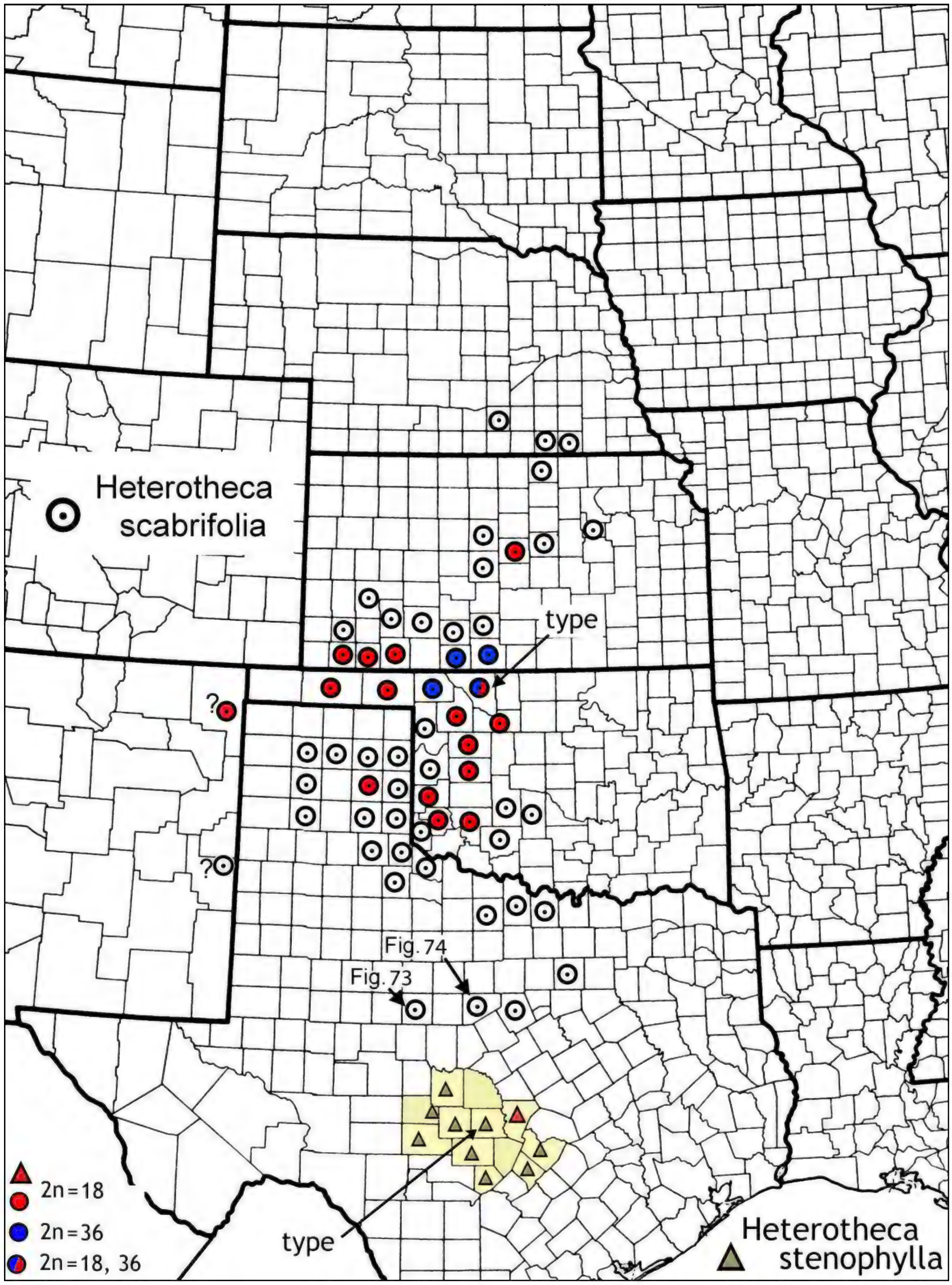


Figure 59. Distribution of *Heterotheca stenophylla* and *H. scabrifolia*, showing locations of diploid and tetraploid chromosome counts. Chromosome data mostly from Harms and Semple. Vouchers for *H. stenophylla* in Kendall and Gillespie counties seen but not recorded/cited. Records for Union Co. and Roosevelt Co., New Mexico, are cited by Harms and Semple but have not been seen in the present study (see text comments). Some Nebraska records added from Kaul et al. (2011, ed. 2). Yellow highlight emphasizes the geography of typical *H. stenophylla*. Collections from Taylor and Eastland counties (see Figs. 73 and 74) apparently are intermediate between the two species.

Figure 60. *Heterotheca stenophylla*, McCulloch Co., Texas, on exposed limestone beside the San Saba River at crossing of Hwy 87 south of Brady (site of *Hansen 7562*, TEX). PhotoS by Nesom, 7 August 2015.

Figure 61. *Heterotheca stenophylla*, McCulloch Co., Texas, same population as in Fig. 45. Large, solitary heads, eglandular phyllaries, densely long-ciliate leaves and capitular bracts. Photo by Nesom, 7 August 2015.

Figure 62. *Heterophylla stenophylla*, from GH isotype, Llano Co., Texas.

Figure 63. *Heterotheca stenophylla*, Travis Co., Texas. *Ertter 5136* (TEX).

Figure 64. *Heterotheca stenophylla*, Burnet Co., Texas, with broad leaves but typical vestiture. *Root 366* (KHD). Similarly broad-leaved forms also have been collected in Hays and Llano counties.

Figure 65. *Heterotheca stenophylla*, Mason Co., Texas. *Hansen 7683* (TEX).

Harms (1963, 1974) cited a single collection of *Heterotheca scabrifolia* (as *H. stenophylla*) from New Mexico and reported it as diploid — Union Co.: 14.5 mi WSW Clayton, *Harms 1862*, **2n=18** (KANU); Semple (1996, 2008) also cited *Harms 1862* as *H. stenophylla*. This specimen is not in the KANU online database nor can it be located at KANU. Semple also cited a collection from Roosevelt Co. as *H. stenophylla* (SW of Clovis, *Harrison s.n.*, GH). I have not seen a collection of typical *H. stenophylla* from New Mexico — it is indicated here (map, Fig. 46), tentatively, as a member of the New Mexico flora.

Heterotheca scabrifolia sometimes grows in close sympatry with *H. canescens* without apparent gene flow. Typical forms of both species were collected at the same locality in Comanche Co., Oklahoma (where both apparently are diploid): Wichita Mts, 3 mi N of Meers, xeric pasture with outcrops of Arbuckle limestone, 21 Oct 1944, *Hopkins & Nelson 812* (WTU, *H. scabrifolia*, stems and leaves glandular and hispid with short, pustulate-based hairs), *814* (WTU, *H. canescens*, stems and leaves densely strigose with long, thin-based hairs).

Harms (1963) found evidence suggesting that tetraploidy in *Heterotheca scabrifolia* in Oklahoma/Kansas may be correlated with slightly larger heads. Offspring of progeny tests from Oklahoma/Kansas *H. scabrifolia* tetraploids produced variants ranging from typical *H. scabrifolia* to typical *H. angustifolia*. *Heterotheca angustifolia* (consistently tetraploid) in the same area shows influence of *H. scabrifolia*.

Similar variability in *Heterotheca angustifolia* of northern Nebraska and adjacent South Dakota (see map, Fig. 40) and Iowa (Lyon Co., e.g., see Figs. 62, 63, 64), fide Harms, suggests that the whole population system in that area is tetraploid and intergrading with *H. angustifolia* (tetraploid counts made from Yankton Co., South Dakota, and Antelope Co., Nebraska). In a 4x Yankton Co. population, Harms found that most plants (89%) were typical *H. angustifolia*; 3% were *H. scabrifolia*. Most plants in Lyon Co., Iowa, have a reduced vestiture similar to *H. scabrifolia* but, following annotations by Harms and Semple, they are identified here as *H. angustifolia*. They have linear-lanceolate leaves with revolute margins and sharply acute apices, sparsely hirsute-strigose to hispid-hirsute with short, pustulate-based hairs, the proximal margins (and bract margins) coarsely ciliate; stems sparsely strigose-hirsute with loose ascending hairs; heads mostly solitary; phyllaries sparsely short-strigose. Plants of the Iowa collections by Gleason and Shimek are glandular, but on plants collected by Fults and by Lassetter neither leaves, stems, nor phyllaries are glandular. Collections from quartzite habitats in Minnehaha Co., South Dakota (e.g., Fig. 65; adjacent to Lyon Co., Iowa), are similar but have longer hairs on stems and leaves and more the aspect of *H. angustifolia*.

Iowa collections (*H. angustifolia*) examined. Lyon Co.: Gitchie Manitou State Park, clumps in the rocks, 14 Sep 1934, *Fults 2940* (WTU); Gitchie Manitou State Park, dry prairie overlying Sioux quartzite, 13 Jul 1940, *Gleason 9374* (SMU); Gitchie Manitou State Park, quartzite outcrop and open area, dry, thin soil, 20 Sep 1969, *Lassetter 1548* (BRY, Fig. 62) and *Lassetter 1560* (BRY, Fig. 63); granite [probably quartzite], no other locality data, 4 Aug 1896, *Shimek s.n.* (MO, Fig. 64); NW corner of county, Sioux quartzite exposures, 25 Aug 1924, *Shimek s.n.* (MO); Gitchie Manitou State Park, prairie bits among Sioux Quartzite exposures, 27 Aug 1932, *Shimek s.n.* (UC).

Figure 66. *Heterotheca scabrifolia*, Ellsworth Co., Kansas. A diploid chromosome count has been made from Ellsworth County. Photo from Kansas Wildflowers and Grasses (www.kswildflower.org/).

Figure 67. *Heterotheca scabrifolia*, Glass Mts., Major Co., Oklahoma. A diploid chromosome count has been made from Major County. Photo by Pieter Pelser, 26 September 2008, used by permission. See Nickrent, D.L., M. Costea, J.F. Barcelona, P.B. Pelser, and K. Nixon. 2006 onwards. PhytoImages. <http://www.phytoimages.siu.edu>.

Figure 68. *Heterotheca scabrifolia*, Texas Co., Oklahoma. *Semple & Shea 2217* (NY). Voucher for a diploid chromosome count. Typical morphology of relatively small, closely clustered heads, short-ciliate leaves and bracts, glandular phyllaries.

Figure 69. *Heterotheca scabrifolia*, Dewey Co., Oklahoma. *Harms 1700* (KANU). Typical morphology. A diploid chromosome count has been made from Dewey County.

Figure 70. *Heterotheca scabrifolia*, Woods Co., Oklahoma. *Harms 1691* (KANU), diploid. The type of *H. scabrifolia* is from Woods County.

Figure 71. *Heterotheca scabrifolia*, Woods Co., Oklahoma. *Harms 1992-B* (KANU), tetraploid. Noted by the collector to be from an intergrading population with *Heterotheca angustifolia*. Diploid and tetraploid chromosome counts have been made from Woods County

Figure 72. *Heterotheca scabrifolia*, Barber Co., Kansas. *McGregor 15105* (KANU), tetraploid.

Figure 73. *Heterotheca scabrifolia*, Taylor Co., Texas, slightly north of the range of *H. stenophylla*. *Johnston 6515* (LL). Small heads in clusters but long-ciliate vestiture more like typical *H. stenophylla*.

Figure 74. *Heterotheca scabrifolia*, Eastland Co., Texas, slightly north of the range of *H. stenophylla*. *Warnock 46387* (TEX). Small heads in clusters (blue arrows) but long-ciliate vestiture more like typical *H. stenophylla*.

Figure 75. *Heterotheca angustifolia*, Lyon Co., Iowa. *Lassetter 1548* (BRY).

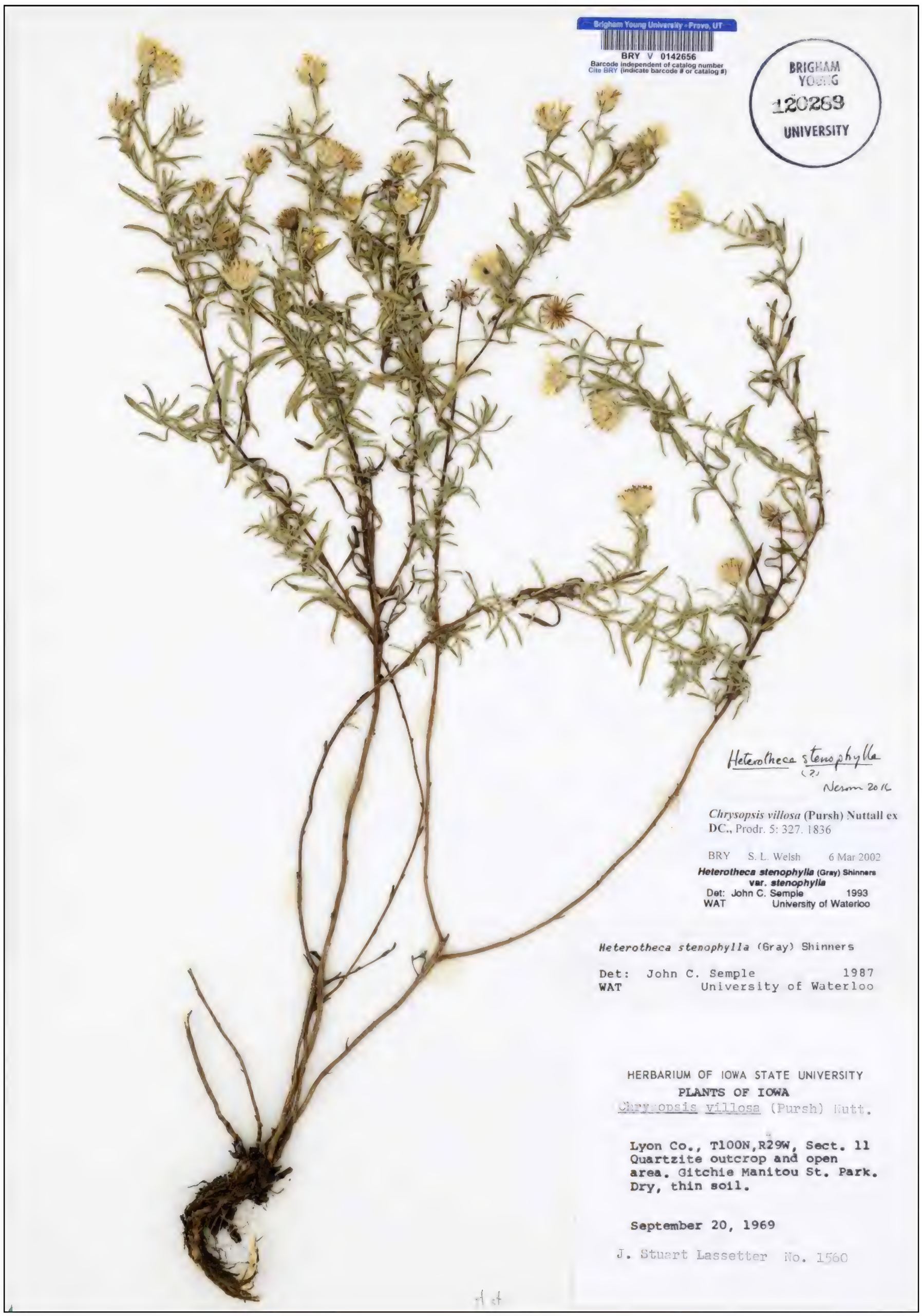


Figure 76. *Heterotheca angustifolia*, Lyon Co., Iowa. *Lassetter 1560* (BRY). See comments in text.

Figure 77. *Heterotheca angustifolia,* Lyon Co., Iowa. *Shimek s.n.* in 1896 (MO).

Figure 78. *Heterotheca angustifolia,* Minnehaha Co., South Dakota. *Stephens 31899* (KANU).

17. HETEROTHECA WISCONSINENSIS (Shinners) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis wisconsinensis* Shinners, Wrightia 1: 218. 1948. **TYPE**: **Wisconsin**. Adams Co.: 15 mi N of Wisconsin Dells on County Trunk D, sandstone bluff, 7 Jul 1947, *H.C. Greene s.n.* (holotype: SMU image!; isotypes: GH, ILL image!, MIL, WIS image!).

Stems stiffly hirsute with spreading to spreading-ascending or slightly deflexed hairs in 2 stories, glandular. **Leaves** oblanceolate to oblong-oblanceolate, (1.6–)20–40 mm, relatively even-sized along the stems or slightly reduced distally, not clasping, conspicuously sessile-glandular, coarsely hirsute, margins long-ciliate. **Heads** essentially solitary (loosely arranged on sparsely leafy peduncles mostly 5–8 cm long), usually with 1 or 2 narrow capitular bracts. **Involucres** 8–10 mm wide; phyllaries villous-strigose to villous-hirsute, glandular. **Ray flowers** 14–30. **Chromosome number** 2*n*=18 (Adams Co., 23 Aug 1987, *Semple 8845*, MO).

Heterotheca wisconsinensis is an unambiguously distinctive species known only from three contiguous Wisconsin counties (Adams, Marquette, and Waushara), which include most of the Wisconsin "Central Sand Plains" (Wisconsin DNR 2014). Other endemics and disjuncts occur in the area. Many collections of *H. wisconsinensis* have been made (see WIS database, where most are currently identified [following Semple 1996] as *H. villosa* var. *minor*). In the protologue of *Chrysopsis wisconsinensis*, Shinners noted that it is "a dwarf spring-flowering [June to early July] plant [and] locally very common and even weedy." More recent collections show that it continues flowering into October but, even so, flowering during spring months is unusual in *Heterotheca*.

Heterotheca wisconsinensis occurs outside of the eastern edge of the range of *H. ballardii*, which is similar in its hirsute stems, oblong-oblanceolate leaves, and heads on relatively long peduncles and subtended by capitular bracts. *Heterotheca wisconsinensis* differs in its more densely hirsute vestiture (often especially noticeable on leaves, bracts, and phyllaries), relatively dense glandularity, much smaller heads, and phyllaries with broad, hyaline margins. Consistent distinctions in vestiture, capitulescence, head size, phyllary morphology, phenology, and disjunct distribution on a specialized habitat provide rationale for the recognition of *H. wisconsinensis* as distinct. *Heterotheca wisconsinensis* is diploid while *H. ballardii* is tetraploid, arguing against a hypothesis that *H. wisconsinensis* originated as a peripheral isolate of *H. ballardii* or of any of the other tetraploid Great Plains populations.

Figure 79. *Heterotheca wisconsinensis*, Adams Co., Wisconsin. *Fassett 16938* (WIS).

Figure 80. *Heterotheca wisconsinensis*, Marquette Co., Wisconsin. *Vazquez G. 5034* (WIS).

18. HETEROTHECA CAMPORUM (Greene) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis camporum* Greene, Pittonia 3: 88. 1896. *Chrysopsis villosa* var. *camporum* (Greene) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca villosa* var. *camporum* (Greene) Wunderlin, Ann. Missouri Bot. Gard. 59: 471. 1973. **TYPE**: **Illinois**. Prairies of Illinois, 1842, *C.W. Short s.n.* (holotype: NDG image!; isotypes: GH image!, NY, US).

Plants taprooted when young, becoming short-rhizomatous (or with short offsets) and fibrous-rooted and losing the taproot, sometimes retaining a woody caudex. **Stems** erect to ascending-erect, 40–70(–150 in var. *glandulissima*) cm; cauline vestiture with strigose understory of loosely appressed hairs, sometimes with sparsely to moderately coarsely hirsute overstory of spreading hairs, eglandular or sparsely glandular. **Leaves**: surfaces moderately hispid to hispid-hirsute or strigose-hirsute to strigose with loosely appressed hairs, eglandular or very sparsely glandular to densely stipitate-glandular. **Heads** without capitular bracts. **Involucres** 7–10 mm high, glandular-viscid, usually without other vestiture, rarely sparsely strigose. **Ray flowers** 16–32(–38); ligules 10–18(–22) mm long, 1–2.2(–2.6) mm wide. **Chromosome number**, $2n$=36.

Semple (1996) separated *Heterotheca camporum* from other goldenasters on the basis of its "stem leaves with several serrate teeth along the margins" ("no other species has well developed serrations along the margins of its upper stem leaves"), relatively tall stature, lack of capitular bracts, and its distribution in the eastern USA.

Harms (1963, p. 52) noted that *Heterotheca camporum* is the "coarsest, tallest, and weediest member of the *H. villosa* complex east of the Rocky Mountains" and characterized the species by "(1) its large size [height], generally exceeding 7 dm, and abundant coarse branching, (2) the distinctly toothed larger leaves, (3) the dense, soft-textured, green foliage, (4) fine, non-pustulate, hirsute primary and secondary stem and leaf pubescence, (5) primary stem hairs displaying a definite, but not pronounced, counterclockwise spiral twisting, (6) very small, distinctly stipitate resin glands, at least on phyllaries and stems, (7) phyllary series rather loose, with at least the inner series recurved at anthesis, (8) large, attenuate rather than petiolate leaves, and (9) large, pedunculate heads in open dichasic cymes, the peduncular leaves reduced, distant, linear, the upper ones grading into phyllaries."

Semple noted (essentially following Harms) that a clinal trend is present in *Heterotheca camporum*, the plants in northern to central Illinois tending to have narrower and more entire leaves, increased glandularity, and longer and more divergent phyllary vestiture. Collections from Carroll, Henry, and Joe Daviess counties identified and mapped by Semple (1993) as forms of *H. villosa* ("aff. var. *minor*" and "aff. var. *villosa*") are the narrow-leaved *H. camporum* (e.g., Jo Daviess Co.: Sand prairie, 18 Aug 1898, *Pepoon s.n.*, PH).

Semple (1983) recognized plants with prominent glandularity as *Heterotheca camporum* var. *glandulissima*, distinguished by "stems that are stipitate-glandular above and that are generally 75 cm tall or more, ... densely stipitate-glandular phyllaries and peduncles that are usually sparsely hispid pubescent, ... moderately to densely glandular and hispid pubescent leaves, and often by having fruits with golden to red-brown translucent ridges." Both varieties are consistently tetraploid ($2n$=36), fide counts by Semple.

Among plants grown from seeds by Harms from a St. Louis, Missouri, population (var. *camporum*), "broad- and narrow-leaved forms appeared, as well as forms with resinous and non-resinous leaves and glabrate and persistently pubescent phyllaries." Five plants of var. *glandulissima* transplanted by the author from Wilson Co., Tennessee (*Nesom het2015-13*), to Fort Worth, Texas, and grown for 3 years did not produce glands on the leaf surfaces.

Figure 81. *Heterotheca camporum*, typical form, Greene Co., Missouri. *Yatskievych 91-280* (MO).

Figure 82. *Heterotheca camporum*, narrow-leaved form, Carroll Co., Illinois. *Thieret 60969* (KNK).

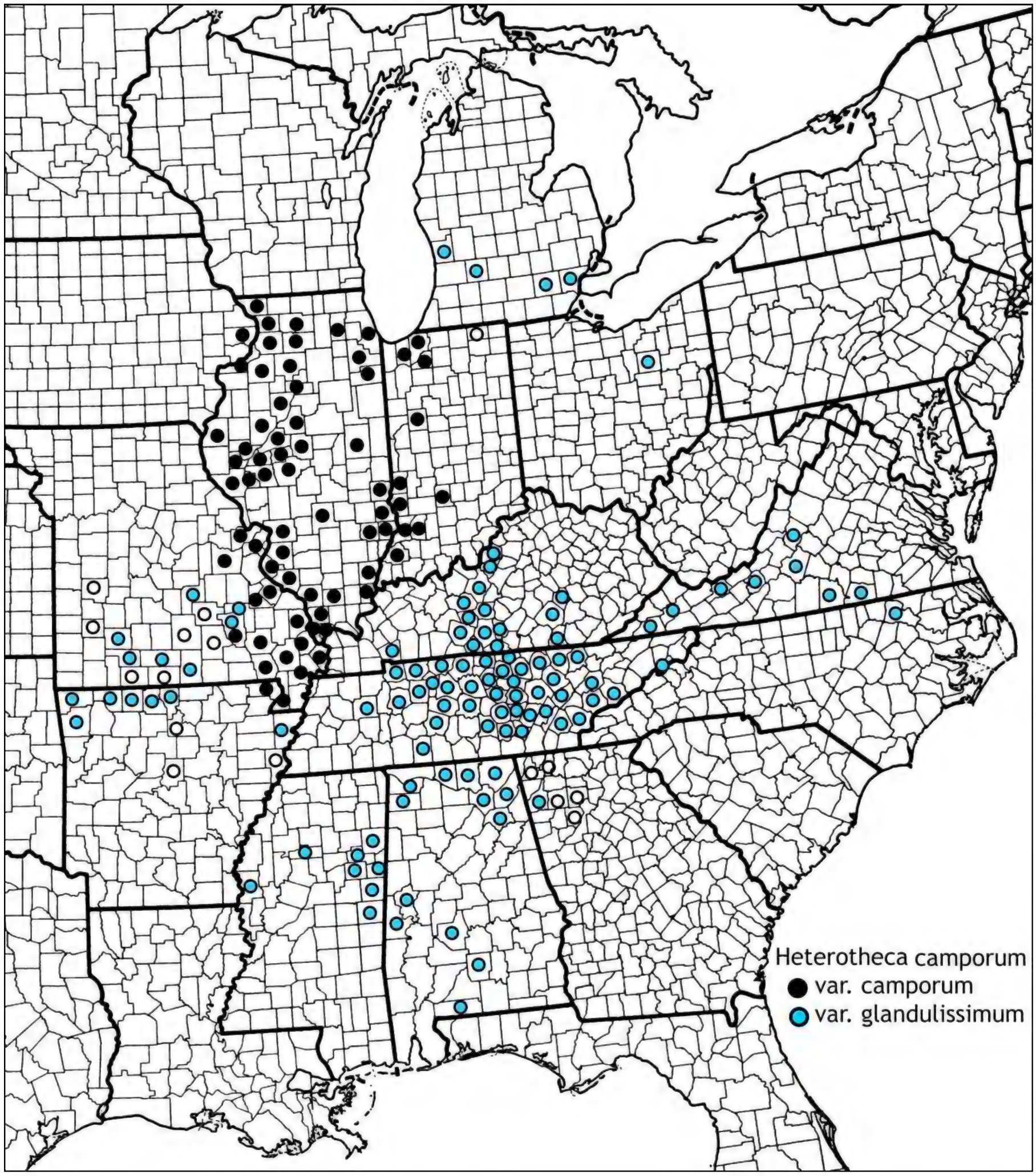


Figure 83. Distribution of *Heterotheca camporum*. Unfilled symbols are records with vouchers not seen by the author.

1. Stems mostly 40–70 cm tall; upper stems and peduncles eglandular to moderately glandular, leaves eglandular ..... 18a. **Heterotheca camporum var. camporum**
1. Stems 65–150 cm tall; stems, peduncles, and leaves prominently stipitate-glandular ..... 18b. **Heterotheca camporum** var. **glandulissima**

18a. Heterotheca camporum var. **camporum**

18b. Heterotheca camporum var. **glandulissima** Semple, Brittonia 35: 146. 1983. *Chrysopsis camporum* var. *glandulissima* (Semple) Cronq., Man. Vasc. Pl. N.E. U.S. (ed. 2), 863. 1991. **TYPE**: **Tennessee**. Cumberland Co.: Protologue and label: Just S of county line along small river, very large population in disturbed sandy soil, 1 Oct 1977, *J.C. Semple et al. 3010* (holotype: WAT; isotypes: MO!, NY image!). Locality from pers. observ., Nesom 2015: 1 mi S of the center of Clarkrange on US Hwy 127, S side of Clear Creek along the Fentress/Cumberland Co. line, large and dense population on steep, clay-loam road bank immediately between the hwy and maintenance road down to the creek, scattered plants on natural limestone ledges and outcrops on adjacent steep slopes with oak-pine woods.

Flowering Jul–Sep(–Oct). Native range as interpreted here (Alabama, Arkansas, Georgia, Kentucky, Mississippi, Missouri, Tennessee): Limestone, shale, and chalk outcrops and bluffs, rocky limestone slopes, rocky roadcuts, cedar glades and barrens, gravelly roadsides and disturbed sites. Outside of the native range (Michigan, North Carolina, Ohio, Virginia, perhaps eastern Tennessee and southeastern Kentucky): roadsides and disturbed sites.

The observations here show essentially the same historical and present distribution of var. *camporum* as mapped by Semple (1983, his Figs. 2-4). The range of var. *glandulissima*, however, is broader than shown by Semple, perhaps reflecting a greater availability of collections.

Semple (1983, 1996) noted that var. *glandulissima* probably was originally adapted to glades and ecologically similar disturbed areas mostly in central Tennessee and adjacent Alabama. Relatively early collections indicate that the original range probably also included limestone/chalk areas in adjacent east-central Mississippi (e.g., Lowndes Co., Columbus, dry ground, 20 Sep 1931, *Sargent s.n.*, LL). Similar sites in south-central Kentucky may also have been part of the original range. Collections from northwestern Georgia are at the southeastern extremity of the native range: e.g., Floyd Co.: Horseleg Mtn, Marshall Forest, rocks, low ridge woods, 800 ft, 17 Oct 1964, *Demaree 51731* (SMU). I see no clear evidence to support Semple's statement (2006, p. 256) that "The variety appears to have evolved within historic times in Tennessee, or only recently to have evolved the traits necessary to make it a successful roadside weed," but it does seem that the species is expanding in geographic range.

Semple (1996) reckoned that the interstate highway system is the primary corridor for migration of var. *glandulissima*. Collectors Sharp and Iwatsuki (*21624*, LL) noted in 1956 that the taxon was a "recent adventive, rapidly spreading" along roadside banks in Putnam Co., Tennessee. Var. *glandulissima* perhaps has recently colonized northwestern Arkansas and south-central Missouri via the road system, but evidence for such a recent range expansion does not seem unambiguous. Railroad rights-of-way may also have facilitated dispersal, e.g., Mississippi Co.: Along RR in Mississippi valley, Frenchman Bayou, 2 Oct 1949, *Demaree 28579* (SMU). Plants identified as var. *glandulissima* have spread northward into Ohio and Michigan and adventive populations are known from North Carolina and Virginia.

The native range of var. *glandulissima* in Tennessee may have been wider than currently supposed (documentation perhaps existed prior to the 1934 fire that destroyed the TENN collection). The species obviously has increased in abundance in Tennessee through creation of roadway-associated habitats, but it also occurs outside of the main "glades" area in what appear to be natural habitats — limestone bluffs, ledges, outcrops, and rocky slopes (pers. observ.). Such is the case at the type locality in Cumberland County, where a large and conspicuous population is established on a clearly man-made habitat, but other plants are scattered on rocky microsites in undisturbed woods on steep slopes of the surrounding area. It also may be true of Putnam County (see comment above

regarding its recent spread there), where plants can be found in undisturbed microsites (pers. observ. 2015).

Notable variants occur on chalk outcrop areas in Sumter Co., west-central Alabama, and in nearly adjacent Oktibbeha Co., Mississippi. In Sumter Co., most collections document glandular plants (e.g., *Thomas 113860*-BRIT, *Kral 48762*-VDB, *Kral 49779*-VDB), but *Kral 29864* (SMU, VDB) has eglandular stems, leaves, and phyllaries. In Oktibbeha County, *Leidolf 1596* (BRIT, VDB) is glandular while *Bryson 8318* (VDB) and *McDaniel 22925* (BRIT, VDB) are eglandular. All of these collections are identified here as var. *glandulissima*, based on their geography.

19. HETEROTHECA BRANDEGEEI (B.L. Rob. & Greenm.) Semple, Syst. Bot. 13: 557. 1988. *Chrysopsis brandegeei* B.L. Rob. & Greenm., Proc. Amer. Acad. Arts 32: 43. 1897 [published 1896]. **TYPE**: **MEXICO**. **Baja California**. San Pedro Mártir, May 1893, *T.S. Brandegee s.n.* (holotype: GH image!; isotypes: OSC image!, RM-fragment!).

Heterotheca martirensis R. Moran, Trans. San Diego Soc. Nat. Hist. 15: 289. 1969. **TYPE**: **MEXICO**. **Baja California**. Sierra San Pedro Mártir, common on N slope of "Cerro 2828," 2800 m, 14 Sep 1968, *R. Moran 15612* (holotype: SD; isotypes: CAS!, GH, K, MICH, NY, RSA!, US). Images! of all types.

Heterotheca brandegeei is endemic to the Sierra San Pedro de Mártir in Baja California (map in Fig. 1). It is characterized by its tendency to produce slender, scale-leaved rhizomes (or rhizome-like caudex branches), leaves mostly crowded toward the branch tips, solitary, rayless heads on long (2–5 cm), bracteate peduncles without capitular bracts, glabrous phyllaries, and hispid-pilose to hirsute-pilose vestiture of stems and leaves. As observed by Semple (1996), this species, apparently allopatric with all others, exhibits a wide range of density of glandular and non-glandular hairs. It offers an unambiguous view of such variability within a single goldenaster species, presumably without genetic influence (at least contemporary influence) from any other.

Semple (1996) noted that the long peduncles and purple-tinged phyllaries of *Heterotheca brandegeei* suggest a relationship with the "Mucronata group" of continental Mexico, while Moran (1969) emphasized its similarities to *H. jonesii* of southern Utah.

20. HETEROTHECA JONESII (Blake) Welsh & Atwood, Great Basin Naturalist 35: 336. 1975 [1976]. *Chrysopsis jonesii* Blake, nom. nov., Contr. U.S. Natl. Herb. 25: 537. 1925; replacing *Chrysopsis caespitosa* M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5: 694. 1895 [not *Chrysopsis caespitosa* Nutt. 1834]. **TYPE**: **Utah**. Washington Co.: Springdale, in red sand, 4000 ft, 16 May 1894, *M.E. Jones 5249u* (holotype: RSA!; isotype: US image!). The RSA branch perhaps was originally part of the much larger plant on the US sheet.

Heterotheca jonesii is restricted to Garfield, Kane, and Washington counties of southwestern Utah (Map 11, Fig. 106), where it occurs in sandy habitats, often in sandstone crevices. The plants are low (2–6 cm high) and commonly form small cushions, with lateral shoots arising from bracteate (scale-leaved), rhizome-like caudex branches. **Stems** and peduncles loosely strigose-villous, understory eglandular, overstory hispid-hirsute. **Leaves** eglandular, loosely strigose-villous with long-ciliate proximal margins. **Heads** solitary on densely leafy stems, capitular bracts little reduced if any from the leaves. **Involucres** relatively small (5–7 mm long), phyllaries often with purplish margins. **Ray flowers** 7–11, ligules drying purplish. **Chromosome number**, $2n$=18.

21. HETEROTHECA LOBOENSIS Nesom, **sp. nov. TYPE**: **Texas**. Culberson Co.: Lobo [16 mi SSE of Van Horn on Hwy 90], roadside with Johnson grass, [4040 ft], 20 Sep 1968, *A.M. Powell 1633* (holotype: TEX, Fig. 85; isotypes: SRSC, USCH image).

Distinct in its tall, erect stems unbranched until above the middle, cauline leaves even-sized and evenly distributed, obovate-petiolate with a rounded and distinctly apiculate apex, heads usually numerous in a corymboid arrangement, on naked or bracteate peduncles. Different from *H. zionensis* in its more sparse and hirsute vestiture of coarser, thick-based hairs, leaf surfaces more densely sessile-glandular, and larger heads on longer peduncles. Different from *H. arizonica* and *H. fulcrata* in lack of capitular bracts and from *H. fulcrata* in its more erect, highly branched stems with more numerous heads.

Stems erect from the base, (10–)20–60 cm tall, hirsute to strigose-hirsute; axillary fascicles (distal nodes) of small leaves usually evident in earlier season plants. **Leaves** cauline, basal petiolate, usually not persistent, relatively even-sized above the basal and evenly distributed, spreading to ascending, midstem and distal basally attenuate but without a distinct petiole, mostly obovate to oblong-obovate or oblanceolate, 9–14 mm long, 4–7 mm wide, apex rounded to truncate and distinctly apiculate, surfaces strigose-hirsute to hirsute-strigose, ciliate or eciliate, glandular adaxially. **Heads** usually numerous in a corymboid arrangement, on naked or bracteate peduncles, without capitular bracts. **Involucres** turbinate-campanulate, 7–9 mm wide (pressed); phyllaries linear-lanceolate, in 4–5(–6) series strongly graduate in length. **Ray flowers** 18–25.

Flowering Jun–Sep. Rocky hills, mesas, canyon bottoms, crevices, roadsides, sand, alluvial silt, igneous and limestone soil, volcanic rocks, desert scrub with *Larrea*; 3900–4500(–6100) ft.

Additional collections. **New Mexico**. Chavez Co. [label says "Otero"]: W side of Guadalupe Mts, 3 mi W of Lincoln Natl forest, T20S R17E, Sec 4, 5800 ft, 10 Aug 1977, *Fletcher 2472* (UNM, Fig. 88b). **Texas**. Brewster Co.: Top of Elephant Mesa on Nevill ranch [now Elephant Mountain WMA] ca. 35 mi S of Alpine, dark volcanic rock, ca. 6100 ft, 20 Jun 1961, *Johnston 6424* (LL). Culberson Co.: Ca. 3 mi E of Van Horn, Hwy 80, sand, 3900 ft, 29 Aug 1947, *Hinckley 4024* (NY); Hurd's Draw [or Herds Pass Draw, ca. 32 mi E of Van Horn], buff silt (alluvial cover), hilly topography, [ca. 4300 ft], 9 Jun 1949, *Janszen 40* (TEX); near N end of Van Horn Mts, depression in gravelly calcareous soil, *Larrea-Flourensia*, 16 Jun 1943, *I.M. Johnston 4556* (NY); 12 mi E of Van Horn on IH-10, [ca. 3900 ft], abundant, 24 Jun 1974, *Powell 2782* (SRSC, TEX); Delaware Mts, 6-7 air mi SE of jct US Hwy 62-180 with Texas Hwy 54, near 31° 42' N, 104° 46' 30" W, rocky canyon bottom, 4500-4700 ft, 27 Aug 1994, *Worthington 23429* (SRSC, TEX, UTEP). Presidio Co.: San Esteban Lake, Marfa, [ca. 4400 ft], Jul 1936, *Hinckley s.n.* (TEX-2 sheets); [or Culberson Co.?] W side of Van Horn Mts, ca. 1 mi S of old mica mill, rocky prominences of low foothills, ca. 4300 ft, 20 Sep 1941, *Hinckley 2154* (NY-2 sheets); San Esteban Canyon, rocky crevice, igneous soil, 4400 ft, 28 May 1957, *Warnock 14465* (LL, SRSC). Hudspeth Co.: 2-4 mi W of Allamoore, frequent locally along hwy in limestone soil, 4100 ft, 7 Sep 1955, *Warnock 13660* (LL, SRSC).

Identification of goldenasters in trans-Pecos Texas remains problematic. *Heterotheca fulcrata* and *H. arizonica* apparently intergrade; *H. zionensis* also occurs in the area and may intergrade with *H. fulcrata*. Recognition of *H. loboensis* as a separate entity is a step toward making the trans-Pecos pattern more comprehensible; another undescribed entity may exist.

Heterotheca loboensis is similar to *H. zionensis* in its erect stems branched above the middle bearing a corymboid array of heads and its involucres without peduncular bracts. The latter, however, produces a closely strigose, more dense vestiture of thinner hairs, characteristically silvery-sericeous and with smaller and more inconspicuous sessile glands on the surface, and smaller heads (involucres (5–)6–9 mm wide, with fewer, less graduate phyllaries and fewer ((10–)12–20) rays) on shorter peduncles (compare Fig. 99, *H. zionensis* from Brewster Co., *Warnock W279*). Plants of *H. loboensis* with putative genetic influence of *H. fulcrata* lack immediately subtending capitular bracts, leaves and bracts with prominent marginal cilia, and distal stems with fewer branches and fewer heads — plants from Hurd's Draw in Culberson County (Fig. 90) perhaps show such intermediacy.

Figure 84. Distribution of *Heterotheca loboensis* — Hudspeth, Culberson, Presidio, and Brewster counties, Texas. Inset shows locality in New Mexico. Also see map in Figure 91.

Figure 85. *Heterotheca loboensis*, holotype (TEX).

Figure 86. *Heterotheca loboensis*, west of Allamoore in Hudspeth Co., Texas. *Warnock 13660* (LL).

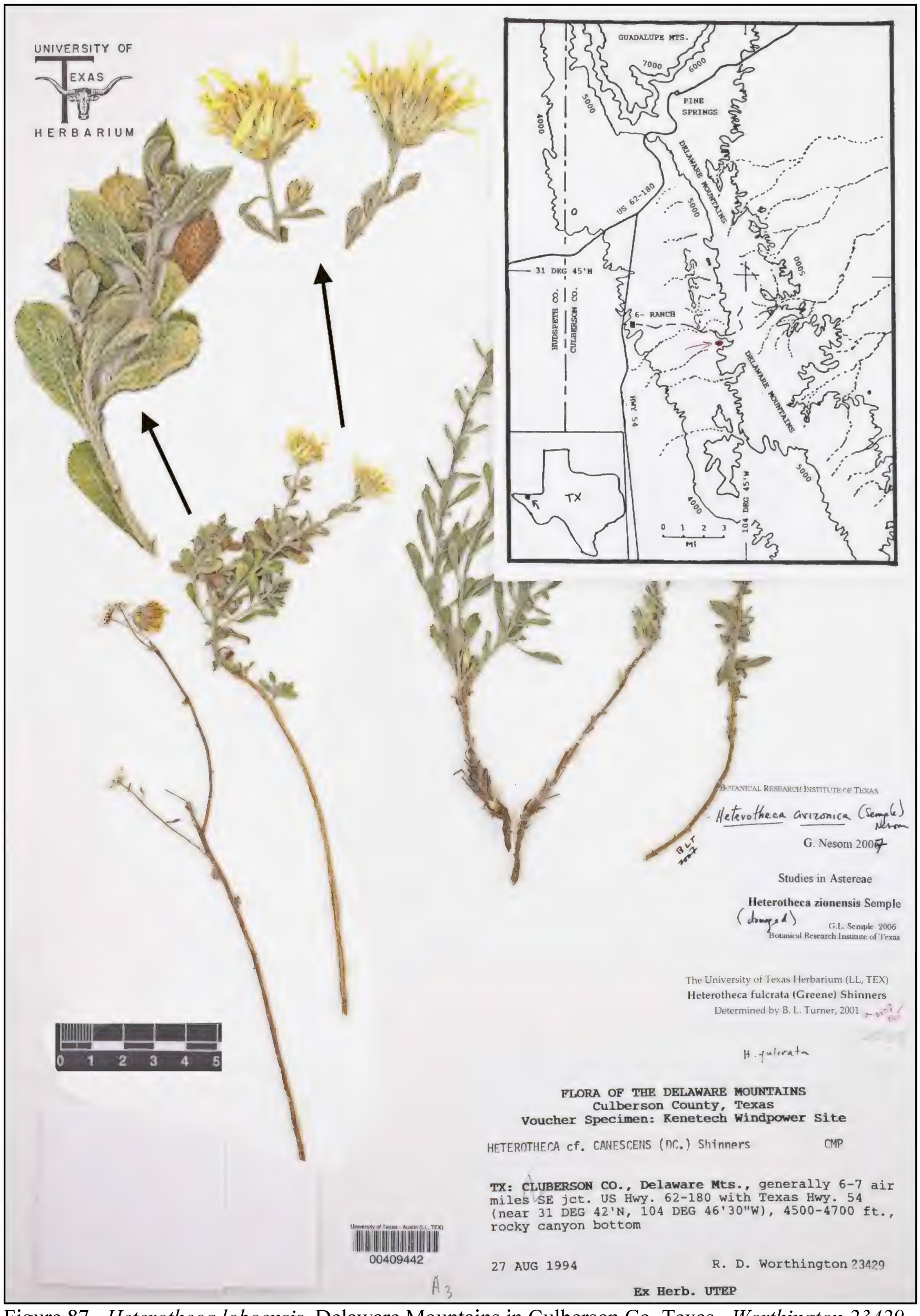


Figure 87. *Heterotheca loboensis*, Delaware Mountains in Culberson Co. Texas. *Worthington 23429* (TEX). Stem height apparently reduced because of drought or stem damage but other features are typical.

Figure 88a. *Heterotheca loboensis*, east of Van Horn in Hudspeth Co. Texas. *Powell 2782* (TEX). Early season form before full development of the inflorescence. Influence of *H. zionensis*?

Figure 88b. *Heterotheca loboensis*, west side of Guadalupe Mts at 5800 ft, Otero Co., New Mexico. *Fletcher 2472* (UNM).

Figure 89. *Heterotheca loboensis*, Elephant Mesa in Brewster Co., Texas. *Johnston 6424* (LL). Peduncles relatively short but other features are more typical. Influence of *H. fulcrata*? (see text comments).

Figure 90. *Heterotheca loboensis* (x *H. fulcrata*?), Hurd's Draw in Culberson Co., Texas. *Janszen 40* (TEX). Stems decumbent-ascending, branches relatively few (but axillary buds prominent — early season?), small, marginally short-cilate subpeduncular bracts present.

22. HETEROTHECA ZIONENSIS Semple, Brittonia 39: 384. 1987. *Chrysopsis zionensis* (Semple) S.L. Welsh, Utah Fl. (ed. 3, rev.), 159. 2003. **TYPE**: **Utah**. Washington Co.: W of Leeds of Silver Reef Road, 3.2 km into Dixie Natl Forest, juniper-sage-yucca, in soft and loose red sand soil, forming dominant local ground cover, 11 Sep 1985, *J. Semple & S. Heard 7859* (holotype: NY image!; isotypes: ASU!). Distribution also to DAO, UTC, and WAT as cited by Semple (1996).

Heterotheca zionensis in characteristic form is identified by its stiffly erect habit, heads in a corymboid arrangement and without capitular bracts, and closely strigose-sericeous, usually silvery (but sometimes more gray) stems, leaves, and phyllaries. Surfaces usually eglandular but sometimes sessile-glandular (under the strigose-sericeous layer). Stem vestiture usually 1-storied (strigose) but sometimes with a much longer, spreading, overstory. Leaves ascending or commonly spreading to deflexed, mostly oblong to oblong-oblanceolate or elliptic with base attenuate to rounded or truncate, sometimes subclasping; axillary fascicles of small leaves usually are evident. Involucres (5–)6–9 mm wide. Ray flowers (10–)12–20. Chromosome numbers, **2*n*=18** (*Semple 7914*, *9018*, *10508*, *10509*; Coconino, Gila, Dona Ana cos., respectively; 8884, Utah Co., Utah; *Ward 81-550*, Dona Ana Co.), **2*n*=36** (*5531*, *9017*, *9022*, *9023*, *9024*, *10493* from Navajo Co.; *9017* from Coconino Co.; *8875* from Wasatch Co., Utah). The tetraploid count of *Semple 8875* is from Midway in Wasatch Co., an area from which I have otherwise seen only collections of *H. utahensis*.

Occasional plants (sometimes perhaps grazed or otherwise damaged) of *Heterotheca zionensis* sometimes are reduced in height and leaf size (vs. the consistently shorter *H. pedunculata*, with which it might be confused in the small region of sympatry) but still distinct in their silvery vestiture, stems arising from the caudex in a dense cluster, and clustered heads.

The range of *Heterotheca zionensis* runs from southwestern Texas through southern New Mexico into Arizona and southern Utah (Garfield, Kane, San Juan, Washington, Wayne cos.). From there it continues, though apparently in less abundance, into north-central and northwest Utah and into northwestern Colorado. In northern Utah, *H. zionensis* is sympatric with plants recognized here as *H. utahensis*. The two are similar in habit and both have been identified by Semple as *H. zionensis*, but they are distinct in vestiture and apparently maintain their identities while occurring in close proximity. Apparent intermediates have been collected but are relatively uncommon: *Semple 8875* occurs in an area where *H. utahensis* is common; *Semple 8884* perhaps shows influence of *H. utahensis*; *Semple 5757* (*E. utahensis*), perhaps shows influence of *H. zionensis*.

a. Stems with closely appressed, 1-storied vestiture, rarely with longer, spreading hairs; leaves usually densely silvery-sericeous, rarely with more reduced vestiture; phyllaries narrowly elliptic-lanceolate to narrowly triangular, closely strigose, eglandular, narrowly elliptic-lanceolate 22. **Heterotheca zionensis**

a. Stems with strigose-hirsute to hirsute, 2-storied vestiture; leaves not silvery sericeous, with non-glandular vestiture not obscuring the surfaces; phyllaries narrowly triangular to linear-triangular, loosely strigose, sessile-glandular at least distally ..... 23. **Heterotheca utahensis**

Collections examined of *H. zionensis* in the northernmost portion of its range. Colorado. Moffat Co.: US Hwy 40, 30 Aug 1930, *Baker 4833* (LL, RM); 20 mi E of Dinosaur near Skull Creek, clay soils, mixed shrub-*Atriplex*-*Oryzopsis* community, 12 Aug 1973, *Higgins 8240* (NY); Pat's Hole, near the confluence of Green and Yampa rivers, dry sandy soil, 4500 ft, 8 Jul 1945, *Porter 3635* (SMU). **Idaho**. Franklin Co.: 1 mi SE of Cleveland, dry slopes, sagebrush-grass, 26 Jul 1952, *Baker 9532* (ID! image!, SRP image!, WTU-3 sheets). **Utah**. Davis Co.: Antelope Island [SE part of Salt Lake near SL City, a peninsula at low lake levels], 4900 ft, 16 Sep 1980, *Clark 4468* (BRY); Antelope Island, 8 Jul 1880, *Jones s.n.* (POM-2 sheets); Antelope Island State Park, W-facing slope 4900 ft, 9 Oct 1983, *Jones 763* (BRY). Salt Lake Co.: City Creek Canyon, open places, 7 Oct 1905, *Garrett 1703* (NY); near Salt Lake City, dry waste ground, 6 Sep 1906, *Garrett 2061* (NY);

between Big and Little Cottonwood canyons, 9 Oct 1909, *Garrett 2653* (LL); Camp Willams Training Area, Traverse Mtn Range, lake terrace, 1494 m, 28 Aug 1993, *Hysell 495* (NY); City Creek Canyon, 6000 ft, Jul 1875, *Jones s.n.* (NY); Little Cottonwood Canyon, along Hwy 152 below Brighton, Storm Mtn quartzite outcrops, Gambel oak, 20 Aug 1983, *Shultz 7233* (NY); Big Cottonwood Canyon, Rte 190 pull-off at "Storm Mtn Quartzite" marker, 1775 m, 29 Jul 2009, *Vincent 14537* (NY). Uintah Co.: Vernal-Manila Hwy, *Garrett 7526* (UT image! and as cited by Semple 1996). Utah Co.: Mt. Timpanogos, Grove Creek canyon, mouth of canyon, dry, rocky soil, 5400 ft, *Allred 366* (BRY); Provo, along Iriquois St., below Rock Canyon flood control dam, ca. 5400 ft, 12 Sep 1983, *Baird 216* (BRY); Provo, dry, gravelly places, sand dunes, 4500 ft, 25 Jun 1925, *Cottam 275* (BRY); East Bench of Provo, dry hillside, 4600 ft, 29 Aug 1932, *Harrison 6123* (BRY); Rock Canyon, dry, rocky slope, 4500 ft, 4 May 1935, *Harrison 7552* (BRY); S of Provo Canyon, inside 1st RH bend of Squaw Peak Road, grassy slope with *Rhus trilobata*, 18 Sep 1980, *Jeppsen 158* (BRY); Utah Hwy 92, 2 km E of Utah Hwy 74 in Alpine, gravel beach and road from dam above, 17 Sep 1987, **2*n*=18**, *Semple & Chmielewski 8884* (BRIT, BRY, MO, UC); SE of Ironton, steep, W-facing slope, 2 Sep 1965, *Welsh 5105* (BRY); Diamond Fork Canyon, ca. 5 mi E of US Hwy 50-6, disturbed, S-facing, gravelly slope, *Artemisia* community, 30 Aug 1967, *Welsh et al. 6640* (BRY). Wasatch Co.: Luke's Hot Pot, Midway, 22 Jul 1927, *Harris C27312* (MO, POM); along East Abish loop road, ca. 16 mi ESE of Heber City, 7710 ft, 5 Aug 2008, *Herrin 248* (BRY); Utah Hwy 220 near intersection with Lime Canyon Road [in Midway], on hot springs margins, in "Hot Pots," 17 Sep 1987, *Semple & Chmielewski 8875*, **2n=36** (BRY, MO). Wayne Co.: Boulder Mtn to Burr Trail to Notom Road, SE of Oak Creek Campground, mountain meadow, 8800 ft, 24 Jul 1973, *Harrison 1275* (BRY); Anderson Bottom, Green River, ca. 3950 ft, 11 Oct 1983, *Welsh 22617* (BRY). Weber Co.: Roy, weed in fields and waste places, sandy, 4200 ft, 19 Jul 1972, *Clark 2238* (BRY); Willard Bay State Park along bay levy, 10 Aug 2000, *Spencer 1565* (NY).

A collection from Mohave Co., Arizona, identified and mapped here as *Heterotheca zionensis*, has the stem and leaf aspect and vestiture of the species, but phyllaries are sessile-glandular, without non-glandular hairs — it perhaps shows genetic influence of *H. cinerascens* where the ranges of the two species meet. Mohave Co.: Ariz 389, 6 mi from Utah border, common along roadside, 5100 ft, 5 Aug 1970, *Holmgren 4661* (ID, RSA, TEX). Collections of typical *H. zionensis* also have been made from Mohave Co.: e.g., Cottonwood Canyon, 23 Jun 2004, *Higgins 25811* (BRY); Cottonwood Canyon, 5 Sep 1978, *Gierisch 4472* (BRY-2 sheets); base of Black Rock Mtn, NE of Jacobs Well, 6 Aug 1980, *Bundy 171* (BRY).

Heterotheca zionensis is adventive in some areas of the city of Santa Fe, New Mexico, where it grows conspicuously and abundantly along street medians and sides (pers. observ.).

Apparent hybrids between *Heterotheca zionensis* and *H. fulciens* have been collected in the Flagstaff area, where both occur abundantly in typical form: *Nelson 63653* (RM) and *Nelson 70314* (RM) have the habit and appressed leaf vestiture of *H. zionensis* but have small capitular bracts and spreading stem vestiture; *Hartman 80060* (RM) has the habit of *H. zionensis* but very small capitular bracts and general vestiture of *H. fulciens*.

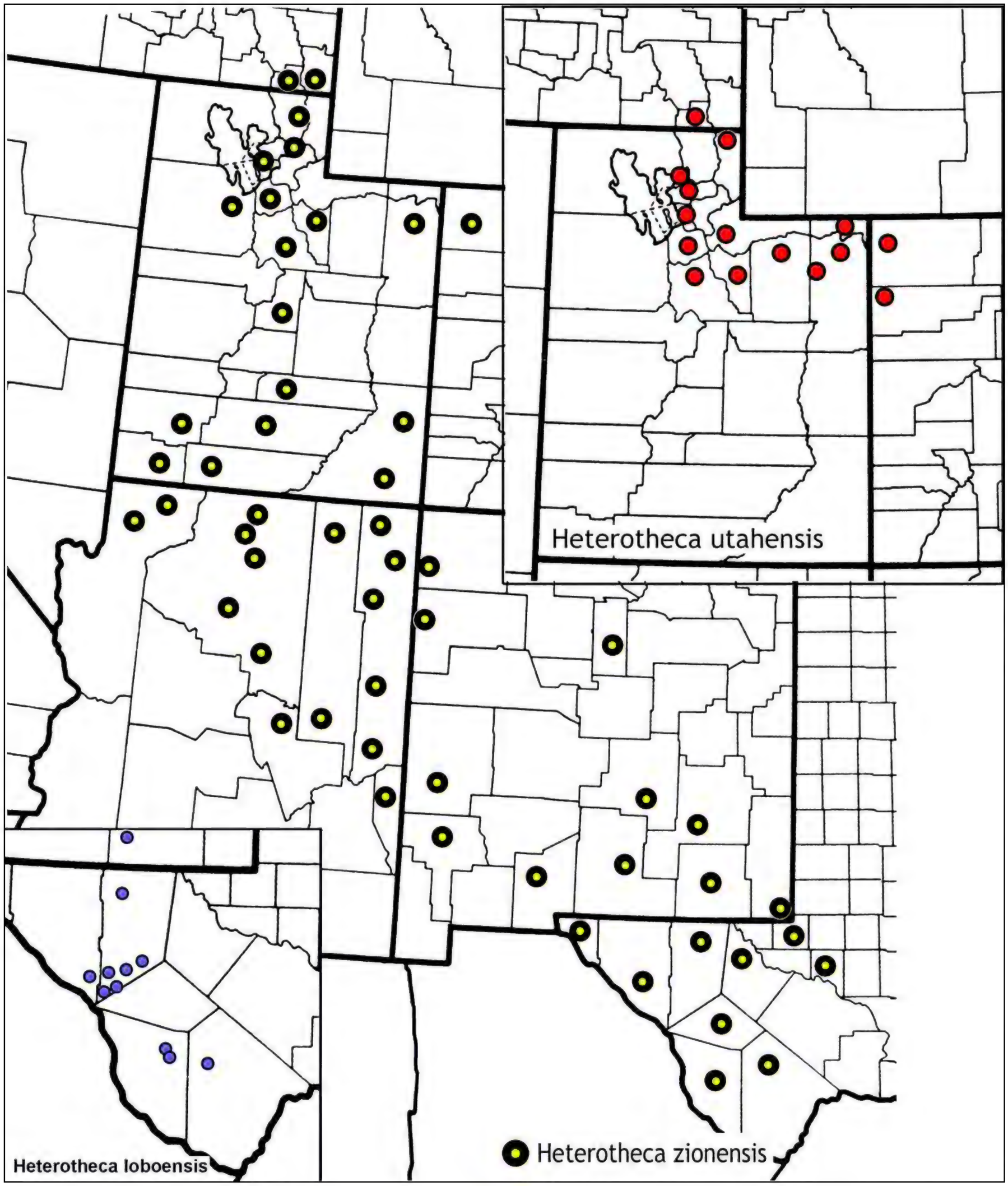


Figure 91. Distribution of *Heterotheca zionensis*, *H. utahensis*, and *H. loboensis*. New Mexico locality is in Chavez Co., at northwest end of Guadalupe Mts., see text and detailed map in Fig. 84.

Figure 92. *Heterotheca zionensis*, Washington Co., Utah. *Higgins 14007* (BRY).

Figure 93. *Heterotheca zionensis*, Coconino Co., Arizona. *Baker 12670* (ASC).

Figure 94. *Heterotheca zionensis*, Kane Co., Utah. *Fertig 27837* (UT).

Figure 95. *Heterotheca zionensis*, Navajo Co., Arizona. *Lehto et al. L19002* (ASU).

Figure 96. *Heterotheca zionensis*, San Juan Co., New Mexico. *Harris s.n.* (UNM). Low habit and rhizome-like caudex branches are unsual, perhaps in response to damage from grazing.

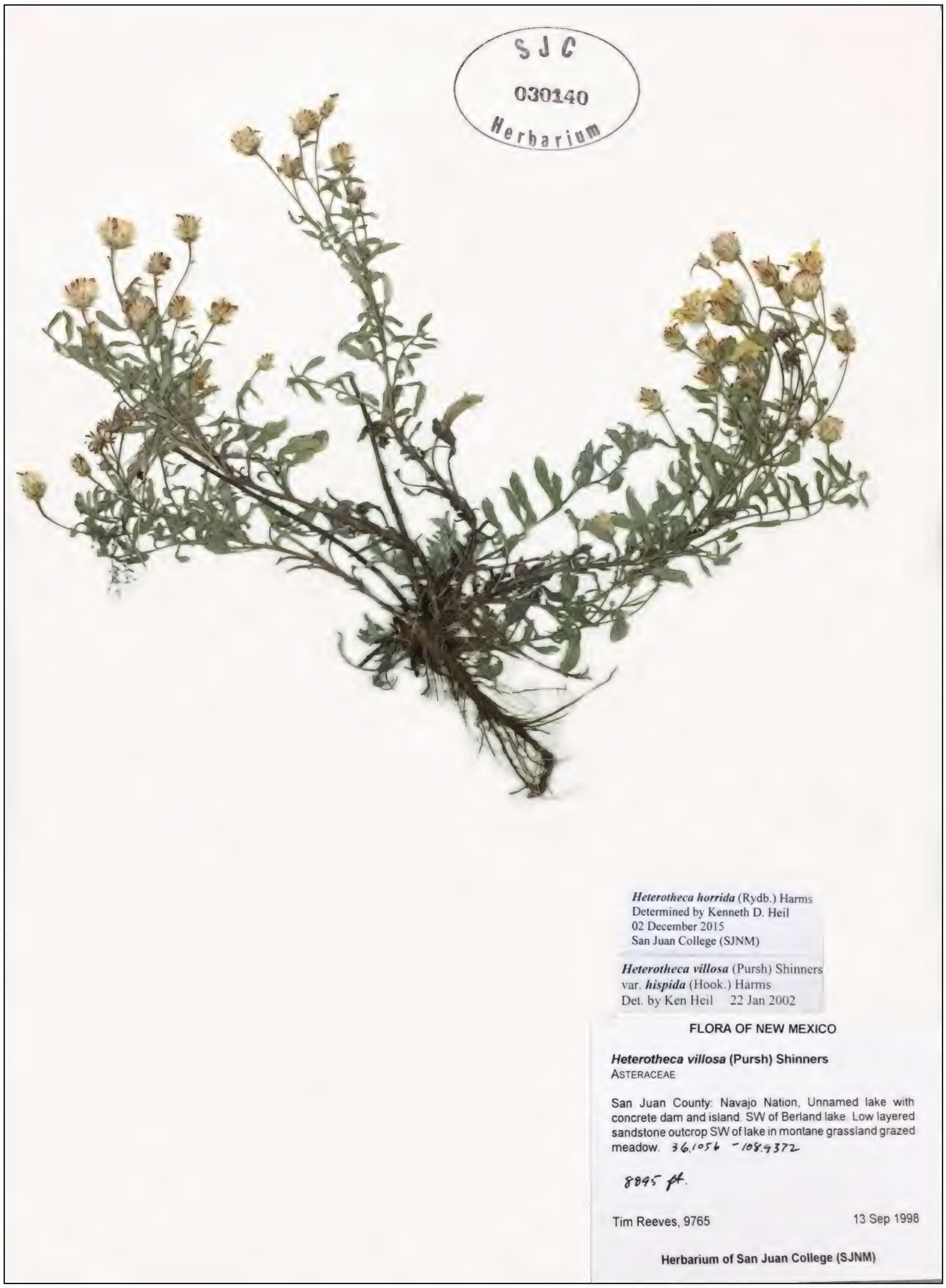


Figure 97. *Heterotheca zionensis*, San Juan Co., New Mexico. *Reeves 9765* (SJNM). Relatively sparse vestiture results in greener color. Depressed habit probably from grazing.

Figure 98. *Heterotheca zionensis*, Roosevelt Co., New Mexico. *Bleakley & DeBruin* 321 (UNM). Influence of *H. angustifolia*?

Figure 99. *Heterotheca zionensis*, Brewster Co., Texas. *Warnock W279* (TEX).

23. HETEROTHECA UTAHENSIS Nesom, **sp. nov. TYPE**: **Utah**. Utah Co.: Lakeview [part of Orem], crest of partially stabilized sand dune, 4500 ft, 24 Jun 1938, *B.F. Harrison 8387* (holotype: UC!).

Similar to *Heterotheca zionensis* in its relatively tall and erect stems often with prominent axillary fascicles of leaves, its oblong to oblong-elliptic, strigose leaves, and its heads in a corymboid arrangement, without capitular bracts; different in its (a) consistently 2-storied stem vestiture, the longer hairs spreading to deflexed, the shorter spreading to ascending, (b) leaves rounded or obtuse to truncate (vs. attenuate) at base, (c) leaf surfaces less densely strigose (not silvery-sericeous) and minutely but prominently and densely sessile-glandular (visible through the non-glandular hairs), and (d) achenes less densely sericeous and with finer hairs.

Perennials from a thick, woody taproot. **Stems** numerous from the base, (12–)20–80 cm, vestiture strigose-hirsute to hirsute, 2-storied, overstory spreading to slightly deflexed, shorter understory spreading to loosely strigose, surface usually prominently sessile-glandular and visible through non-glandular hairs. **Leaves** usually densely arranged and even-sized, ascending or commonly spreading to deflexed, mostly oblong to oblong-elliptic or oblong-oblanceolate to elliptic, 10–30(–40) x 4–13 mm, mid and distal cauline usually narrowed to a subpetiolate base, not clasping or subclasping, distally becoming epetiolate with base rounded to truncate, sometimes subclasping, apex mostly truncate to rounded, sometimes acute, often apiculate; axillary fascicles of small leaves prominent and consistently produced. **Heads** usually numerous in a corymboid arrangement, without capitular bracts, peduncles relatively short, (2–)5–15(–30) cm. **Involucres** 7–10 mm wide (pressed); phyllaries sparsely loosely strigose, commonly purple-tipped, outer often sessile-glandular at least distally, inner 7–8 mm long, narrowly triangular to linear-triangular. **Ray flowers** 12–25. **Chromosome number**, 2*n*=36 (*Semple & Chmielewski 8887*, Utah Co., Utah).

Heterotheca utahensis is endemic to northern Utah and immediately adjacent Idaho and Colorado. *Heterotheca zionensis* and *H. utahensis* perhaps are closely related evolutionarily but plants of intermediate morphology are not common, suggesting that an isolating mechanism is in effect. I identified the BRY sheet of *Spencer 1565* from Weber County as *H. utahensis* but the NY sheet as *H. zionensis*. The 'utahensis' entity is limited in geography (it does not occur over most of the range of *H. zionensis*), further indicating its genetic distinction.

Additional collections examined. Colorado. Moffatt Co.: "Western Colorado, along Hwy 40," 30 Aug 1930, *Baker 4833a* (LL, RM; Semple annotated the LL specimen as *H. zionensis* with the following comment: "like N Utah 4x plants" ... "? Introduced from Provo-St. Lake UT area."); along Yampa Rd, 2-3 mi SE of Hwy 40 bridge SE of Maybell, brushland area with narrow riparian corridor, 4 aug 1991, *Keil 22511* (OBI); "14" at Disappointment Draw, sagebrush, 6000 ft, 19 Jun 2002, *Tilley 2823* (BRY). Rio Blanco Co.: ca. 18 mi E of Dinosaur, salt desert shrub community, 5640 ft, 10 Aug 1979, *Welsh & Moore 312* (BRY). **Idaho**. Franklin Co. Maple Grove Hot Springs, Oneida Reservoir, ca. 21 mi NE of Preston, travertine, 4900 ft, 9 Jul 1961, *Bright 61-46* (RM); Franklin Basin, White Canyon, 8300 ft, 30 Jul 1958, *Cottam et al. 15304* (BRY). **Utah**. Box Elder Co.: 8 mi S of Brigham City, US 89 and 91 S of Willard, more or less disturbed ground on dry, open slope between mtn and road, ca. 4350 ft, 18 Aug 1963, *Rossbach 5560* (WTU). Daggett Co.: Near mouth of Cart Creek, woodland, 5500 ft, 29 Jul 1929, *Hutchings 117* (RM); ca. 8.5 air mi S of Manila, ca. 4.5 road mi W of Utah Hwy 44 on both sides of Forest Rd 539, sagebrush and pine, 7780-7900 ft, 30 Jun 1994, *Refsdal 1404* (RM); Flaming Gorge Natl Rec Area, Carter Creek, ca. 8.1 air mi S of Manila on N side of Utah Hwy 44, pine-juniper, 7200-7300 ft, 2 Sep 1995, *Refsdal 7857* (RM). Davis Co.: Davis County Watershed Terraces on Bountiful Peak, 8 Sep 1972, *Allan 224* (BRY); Goat Ranch, N of Rock Creek-Bountiful, 5000 ft, 25 Jun 1959, *Cottam et al. 15570* (DS, RSA, UT); U.P. right-of- way, Farmington, introduced and locally common in dry sandy soil, 13 Jul 1951, *Holmgren 8258* (CAS, DS, RM, RSA, UC, WS, WTU); Union Pacific right-of-way, 3/4 mi S of Farmington, 16 Jul 1951, *Kendrick K-1* (RM-2 sheets); 2 mi N of Farmington Jct, US Hwy 89, frequent on sandy benches with scrub oak, 7 Sep 1940, *Maguire 20117* (WTU). Duchesne Co.: Along Big

Cottonwood draw–Boneta, 26 Jul 1981, *Brotherson 3356* (BRY); 5.5 mi due NW of Altamont, juniper-sagebrush, glacial outwash, 6940

Figure 100. *Heterotheca utahensis*. Salt Lake Co., Utah. *M.E. Jones s.n.* (MISSA).

Figure 101. *Heterotheca utahensis*, Salt Lake Co., Utah. *Garrett 6980* (KANU).

Figure 102. *Heterotheca utahensis*, Salt Lake Co., Utah. *Garrett 6980* (UT 0119750).

Figure 103. *Heterotheca utahensis*, Davis Co., Utah. *Cottam et al. 15570* (UT).

ft, 24 Jul 1984, *Goodrich 20987* (BRY); Uintah Mts, Hells Canyon, 28 mi from Duchesne, lodgepole pine-aspen, 8800 ft, 21 Jul 1989, *Goodrich 22968* (BRY). Rich Co.: Bear Lake, [ca. 6500 ft], 14 Aug 1933, *Flowers F1683* (LL). Salt Lake Co.: Red Butte Canyon, E of Salt Lake City, disturbed flat area near road opposite main reservoir, 5400 ft, 19 Jul 1968, *Arnow 2117* (BRY); Traverse Mts, Corner Canyon, rocky S-facing slope, 5000 ft, 7 Aug 1988, *Arnow 6501* (MO); Fort Douglas, 27 Sep 1909, *Clemens s.n.* (RM, UC); Little Cottonwood Canyon, 9 Oct 1909, *Clemens s.n.* (CAS, UC); near Salt Lake City, 7 Oct 1905, *Garrett 1709* (DS, RM); E of Draper, foot of hillsides, 21 Jun 1934, *Garrett 6619* (DS, SMU); Salt Lake City, 4400 ft, 16 Sep 1934, *Garrett 6847* (UC); Salt Lake City, Lindsay's Garden, 4700 ft, 17 Jul 1935, *Garrett 6980* (KANU, UT); Salt Lake City, 17 Jul 1880, *Jones s.n.* (POM); Alta, 7400 ft, Aug 1879, *Jones 1383* (NY); Wasatch Mts, 8 Aug 1882, *Jones s.n.* (MISSA image!); near Salt Lake City, 5 Aug 1872, *Redfield 2974* (MO); Little Cottonwood Canyon, along Hwy 152 below Brighton, outcrop of quartzite, scrub oak (*Q. gambelii*), 20 Aug 1983, *Shultz 7233* (CAS); Cottonwood Canyon, near Salt Lake, 7 Sep 1896, *Stokes s.n.* (DS); 1/3 mi up Big Cottonwood Canyon, 5300 ft, 4 Oct 1955, *Vickery 364* (WTU). Summit Co.: Near Echo Reservoir, 28 Jul 1938, *Garrett 7888* (SMU). Uintah Co.: Fort Duchesne, 1913, *Carter 48* (RM); Red Wash just NW of mouth of Split Mtn Canyon, above Island Park, 5200 ft, 10 Jun 1935, *Graham 9174* (MO); at overlook of Dry Fork Canyon along Red Cloud Loop, aspen-lodgepole pine, 2 Sep 1967, *Welsh & Moore 6747* (BRY). Utah Co.: NE corner of old cemetery [other loc. data not specified], 3900 ft, 14 Jun 1940, *Bird 13B* (BRY); Provo, sand dunes, 4500 ft, 16 Jul 1925, *Cottam 275* (BRY); Thistle, 25 Jun 1918, *Eastwood 7701a* (CAS); W bank of Provo River, 10 mi N of Provo, dry gravelly soil in clearing, 4500 ft, 29 Jul 1949, *Galway 2258G* (BRY-2 sheets, UC); Provo, dry hillside, 12 Jun 1925, *Garrett 3311* (RM); sand dunes W of Provo, 25 Jun 1925, *Garrett 3350* (RM); Lakeview, crest of partially stabilized sand dunes, 4500 ft, 24 Jun 1938, *Harrison 8387* (BRY); Provo [Slate Canyon, gravel], 6000 ft, 10 Jul 1894, *Jones 5613* (MO-2 sheets, NY, POM, UC); shore of Lake Provo, several large populations, common locally in disturbed areas, 11 Sep 1985, *Semple 5757* (BRIT, BRY, MO, UC); 5 km N of University Parkway on UT Hwy 189, just N of Drew Center St., abundant along road between 4000-5000 University Ave, 17 Sep 1987, *Semple & Chmielewski 8887*, **2n=36** (BRIT, MO, UC); Provo Canyon, below Springdale, 23 Jul 1909, *Smith 1926* (DS). Wasatch Co.: Near Midway, 6 Jul 1905, *Carlton & Garrett 6693* (RM); near Deer Creek around edge of sagebrush, dry soil, 5300 ft, 10 Oct 1964, *Foster 210* (BRY); Low Pass Creek, 20 mi E of Heber City, crack of S-facing slab of sandstone with scattered doug fir, juniper, aspen, 8850 ft, 20 Aug 1981, *Goodrich 16104* (BRY); 2 mi W of Heber City on US Hwy 40, steep road embankment, 30 Aug 1981, *Semple 5760* (BRY, MO). Weber Co.: Peterson, Weber River, Devils Gate, 6500 ft, 18-24 Jul 1902, *Pammel & Blackwood 3914* (MO); Willard Bay State Park, along bay levy, 10 Aug 2000, *Spencer et al. 1565* (BRY); North Taylor Canyon, ridge, talus, 30 Nov 1933, *Stewart 40* (RM).

24. HETEROTHECA PEDUNCULATA (Greene) Nesom, **comb. nov.** *Chrysopsis pedunculata* Greene, Pittonia 4: 154. 1900. *Heterotheca villosa* var. *pedunculata* (Greene) Harms ex Semple, Brittonia 39: 383. 1987. **LECTOTYPE** (Semple 1987): **Colorado**. Archuleta Co.: Pagosa Springs, 20 Jul 1899, *C.F. Baker 651* (NDG 53927 image!; isolectotypes: E, F, GH, JE, K, MO-Fig. 109, NDG 53926, NY-Fig. 110, P, RM-2 sheets!, RSA-2 sheets!, UC, US). Images! of all types. See Figs. 74, 75.

Chrysopsis bakeri Greene, Pittonia 4: 154. 1900. **LECTOTYPE** (Semple 1987): **Colorado**. Archuleta Co.: Near Pagosa Peak, 9000 ft, 23 Aug 1899, *C.F. Baker 649* (NDG 53928 image!: isolectotypes: E, GH, MO!, NDG 53768, NDG 53769, NMC, POM!, RM-2 sheets!, UC!, US). Images! of all types except MO.

Heterotheca pedunculata is recognized by its heads without prominent capitular bracts, stems and leaves eglandular and strigose with short, thin-based, closely appressed hairs (sometimes with a sparse, spreading or ascending overstory), and ascending leaves usually oblanceolate and narrowed to a subpetiolar base. Involucres 9–15 mm wide (pressed). Phyllaries narrowly elliptic-lanceolate to narrowly ovate-lanceolate. Rays 10–16. Plants commonly arise from rhizome-like caudex branches and often are collected without a taproot. Semple (1996, p. 124) also saw *H. pedunculata* as a distinct entity: "Semple (1990) included [*Heterotheca villosa* var. *pedunculata*] among tentative synonyms of

var. *villosa*, but the results of multivariate analyses conducted since then indicate that it is sufficiently distinct from var. *villosa* to warrant recognition even when only nondiagnostic traits are used in the discriminant analysis."

A collection of (apparently) *Heterotheca pedunculata* from south-central New Mexico would be far out of range, perhaps reflecting a labeling error: Doña Ana Co.: on the mesa W of the Organ Mts, 4000 ft, 1 Oct 1907, *Wooton s.n.* (DS-2 sheets). It may be an convergent plant of *H. zionensis*, which is known from Doña Ana County by numerous collections.

Tetraploid chromosome counts by Semple for *Heterotheca pedunculata* have been made from Colorado (Archuleta and Montezuma cos.) and Utah (San Juan and Summit cos.). Diploid counts have been made from Colorado (La Plata Co. — 1 population, possibly a hybrid with *H. hirsutissima* — and Montezuma Co. — 1 population, seemingly identical to the tetraploid population from the same area) and from Utah (San Juan Co.).

A population system of plants identified here as *Heterotheca pedunculata* is abundant on the Uncompahgre Plateau in Montrose County at 7900-9450 feet and adjacent Mesa County and Ouray County; e.g., Figs. 120, 121; collections of these are cited below). These plants are consistent in their eglandular, closely strigose leaves, antrorsely but loosely appressed stem vestiture usually with an overstory of long, spreading hairs, and consistent production of a woody or lignescent taproot (the latter more similar to *H. inflata* than to typical *H. pedunculata*). They also differ from typical *H. pedunculata* in their larger leaves, leafy peduncles, and slightly larger heads — the aspect in the field is different from typical *H. pedunculata*.

My personal collections of these "Uncompahgre variants" are identified and distributed as *Heterotheca pedunculata* “perhaps with influence of *H. inflata*”; some other similar collections were annotated as *H. inflata* before I was clear on the nature and geography of the variants. Their morphological distinction is somewhat subtle but it is consistent and geographically coherent — a formal name for these plants appears to be justifiable.

The same variant also occurs at elevations up to 12,000 feet in the nearby La Sal Mountains and Abajo Mountains of Grand and San Juan counties, Utah (e.g., Figs. 122, 123), where some have been identified by Semple (1996) as *Heterotheca pumila* or "aff. *H. pumila*." The leafy peduncles are similar to *H. pumila* but the plants are eglandular, lack capitular bracts, and are out of geographic range for *H. pumila*. I found no *H. pumila* in either of these two areas (pers. observations and collections, 2017).

Heterotheca pedunculata, **"Uncompahgre variant"**

Colorado. Mesa Co.: Off Uranium Road, ca. 2 mi W of Divide Road, mesa and meadow, scattered aspen, 8870 ft, 8 Jul 1994, *Lyon 5626* (RM). Montrose Co.: Dry Creek Trail (Forest Trail 114), along trail and adjoining area, ca 18.5 air mi SW of Montrose, roadside in mixed aspen/coniferous forest, 8840-9520 ft, 6 Jul 2011, *Brummer 4781* (RM); ca. 17.5 road mi SW of Montrose on Road 90, NE of Rim Road jct, ca. 3 mi N of boundary of Uncompahgre Natl Forest (where road becomes numbered as "540"), Gambels oak, sage, *Erigeron speciosus*, *Heliomeris*, 8300 ft, scattered along road banks and woods edge, 19 Aug 2017, *Nesom het17-21* (4 dups); ca. 21 road mi SW of Montrose on Rd 90 (FS Rd 540), ca. 1 mi above (W of) Uncompahgre Natl Forest boundary, just E of jcts to Naturita (FS Rd 540) and to the Dave Wood Rd (Co Rd 402), meadows and openings in aspen-ponderosa pine-fir, 9450 ft, very abundant, full flower, 19 Aug 2017, *Nesom het17-22* (7 dups); Columbine Pass on Divide Rd (FS 540 = Co. Rd 402), NNE of Nucla and Naturita, aspen-spruce-fir-ponderosa pine, 9300 ft, abundant in openings and along roadside, 19 Aug 2017, *Nesom het17-23* (3 dups); ca. 5 mi SE of Columbine Pass on FS Rd 503 toward Nucla, 1 mi S of Tabeguache Creek crossing, ca. 12 air mi NE of Nucla, ponderosa pine-Gambel's oak, 7900 ft, locally abundant on roadbank and roadside, 19 Aug 2017, *Nesom het17-24* (3 dups); Tabeguache Basin, meadows, 9000 ft, 22 Aug 1913, *Payson 205* (RM-2, NY-Fig. 121); 25 mi SW of Montrose, Uncompahgre Plateau, open meadow among spruce, 9500 ft, 5 Sep 1936, *Rollins 1599* (LL, MO, NY-Fig.

120, RM-2 sheets). Ouray Co.: Above East Fork Spring Creek, off of Forest Rd 532, 3.1 road mi N of Divide or Forest Rd 402, ca 17 air mi SSW of Montrose, subalpine meadow, 8810-9100 ft, 24 Jul 2011, *Brummer 5939* (RM); San Juan Mountains, Uncompahgre Natl Forest, Cimarron Ridge, Lou Creek Pass, ridge just S of Lou Creek Pass then W on Lou Creek Pass Trail to ridge above Kennedy Mine, ca 11 air mi NNE of Ridgway, moist meadow in aspen/spruce/fir mix, 9656-11031 ft, 22 Jul 2012, *Brummer 10245* (RM).

Other plants of *Heterotheca pedunculata* with loosely strigose stem vestiture occur in scattered localities and may reflect independent hybrid origins, e.g., Gunnison Co., Roger's, 9000 ft, 14 Aug 1901, *Baker 794* (RM, see Fig. 114; "Roger's" was a stop on the Delta & Rio Grande Railroad, ca. 3 mi W of Crested Butte along what is now Colo Hwy 12 beside Coal Creek). In Ouray Co., some plants of relatively typical *H. pedunculata* have larger heads on long, few-bracteate peduncles — these also may reflect genetic influence of *H. inflata*, but relatively large-headed *H. pedunculata* also occurs within scattered populations elsewhere in its southern range.

Heterotheca pedunculata reaches its southeastern limit in New Mexico. Colfax Co.: 7 mi W of Gladstone, prairie area, roadside, edge of asphalt, [ca. 6100 ft], 14 Jul 1972, *Harms 19111* (KANU, Fig. 118); Vermejo Park Ranch, roadside 0.2 air mi E of Upper Underwood Lakes, near jct with small unnamed side road, dry rocky meadow on S-facing slope on edge of *Pinus aristata* woodland, uncommon, 10,000 ft, 4 Aug 2008, *Legler 10327* (COLO, RM, UNM — Figs. 115, 116, 117). San Miguel Co.: Upper Pecos River, near Willow Creek, 7820 ft, riparian, 7 Aug 1992, *Kirchner 005-F15* (UNM image!).

Figure 104. *Heterotheca pedunculata*, Montezuma Co., Colorado, near Cortez. Photo by Al Schneider, 31 May 2004. Spreading stem hairs are a sparse "overstory" above the closely appressed, strigose layer that give stems and leaves the silvery color.

Figure 105. *Heterotheca pedunculata*. Mineral Co., Colorado, along the East Fork San Juan River. Photos by Rich Haswell, September 2020.

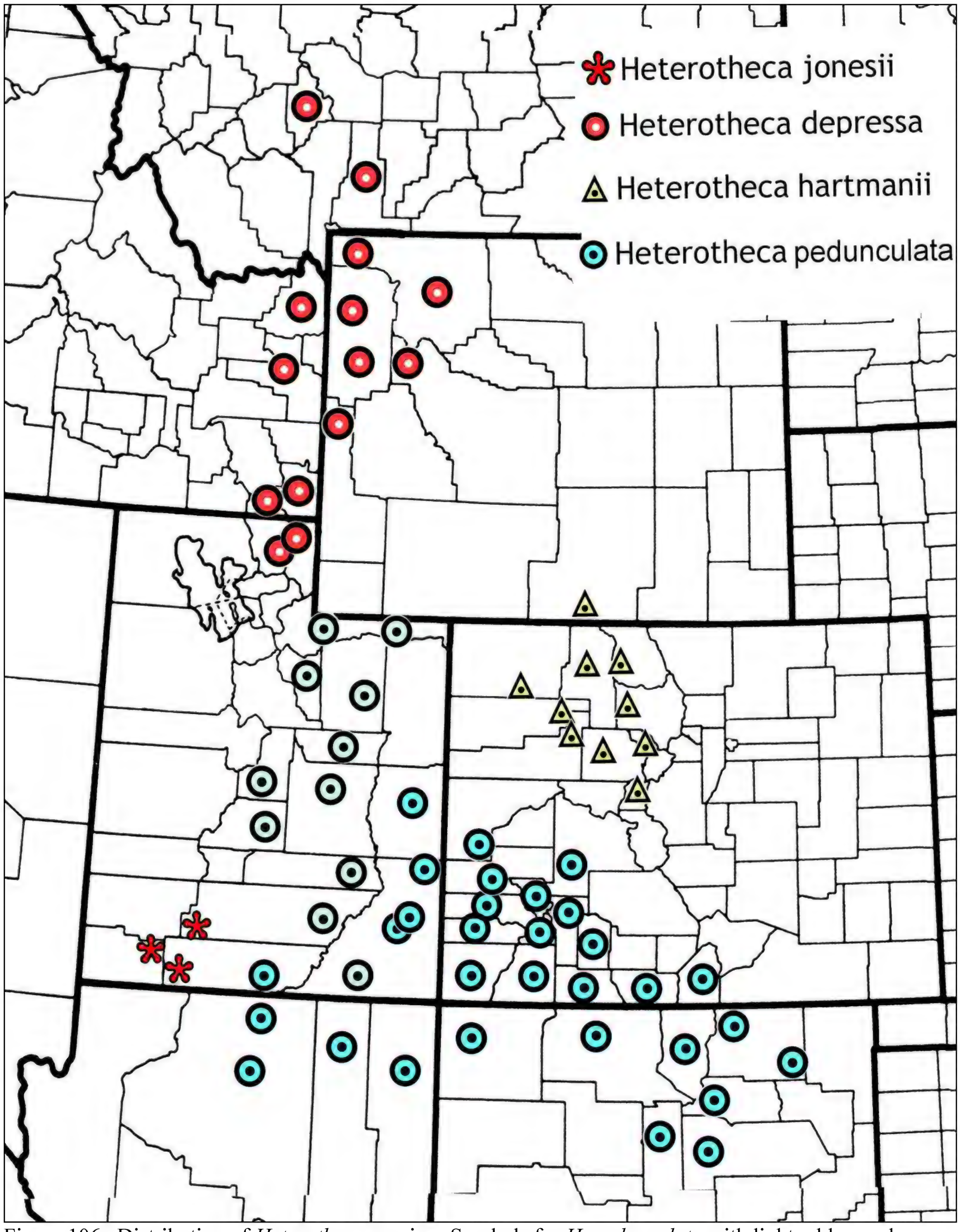


Figure 106. Distribution of *Heterotheca* species. Symbols for *H. pedunculata* with lighter blue perhaps are a different species, yet undescribed. Also see text for comments on the "Uncompahgre variant" of *H. pedunculata*.

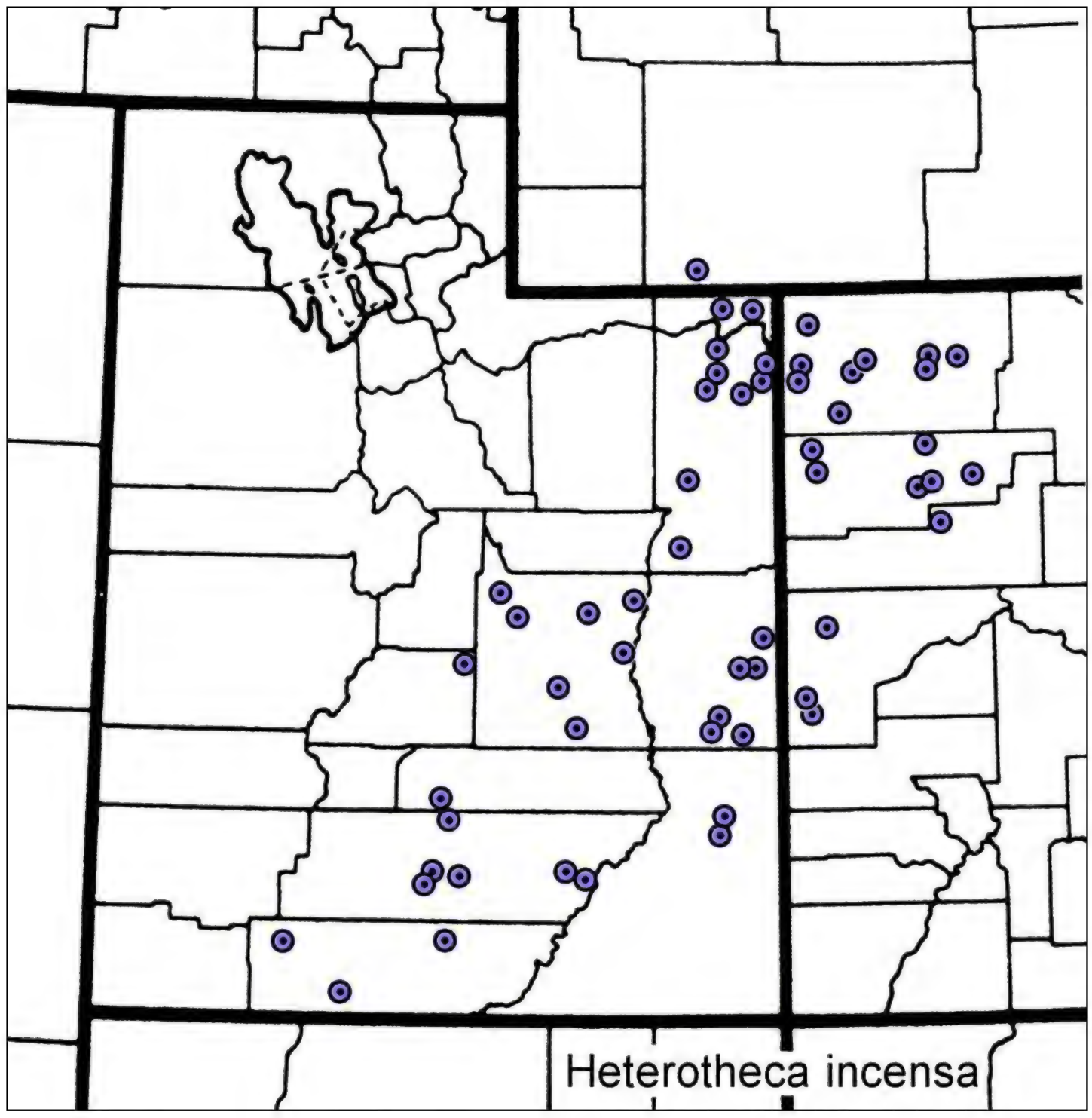


Figure 107. Distribution of *Heterotheca incensa*.

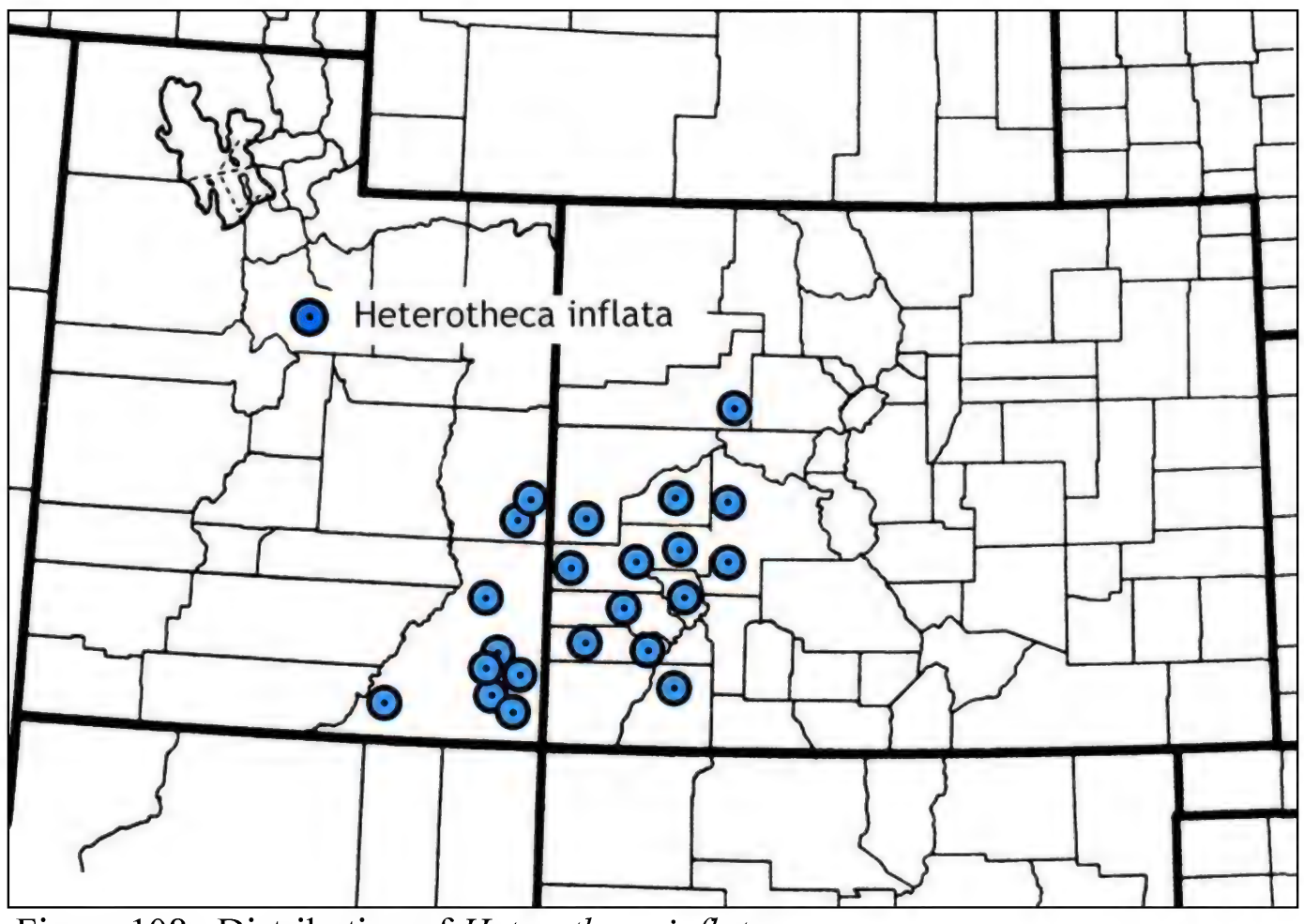


Figure 108. Distribution of *Heterotheca inflata*.

Figure 109. *Heterotheca pedunculata*, isolectotype (MO).

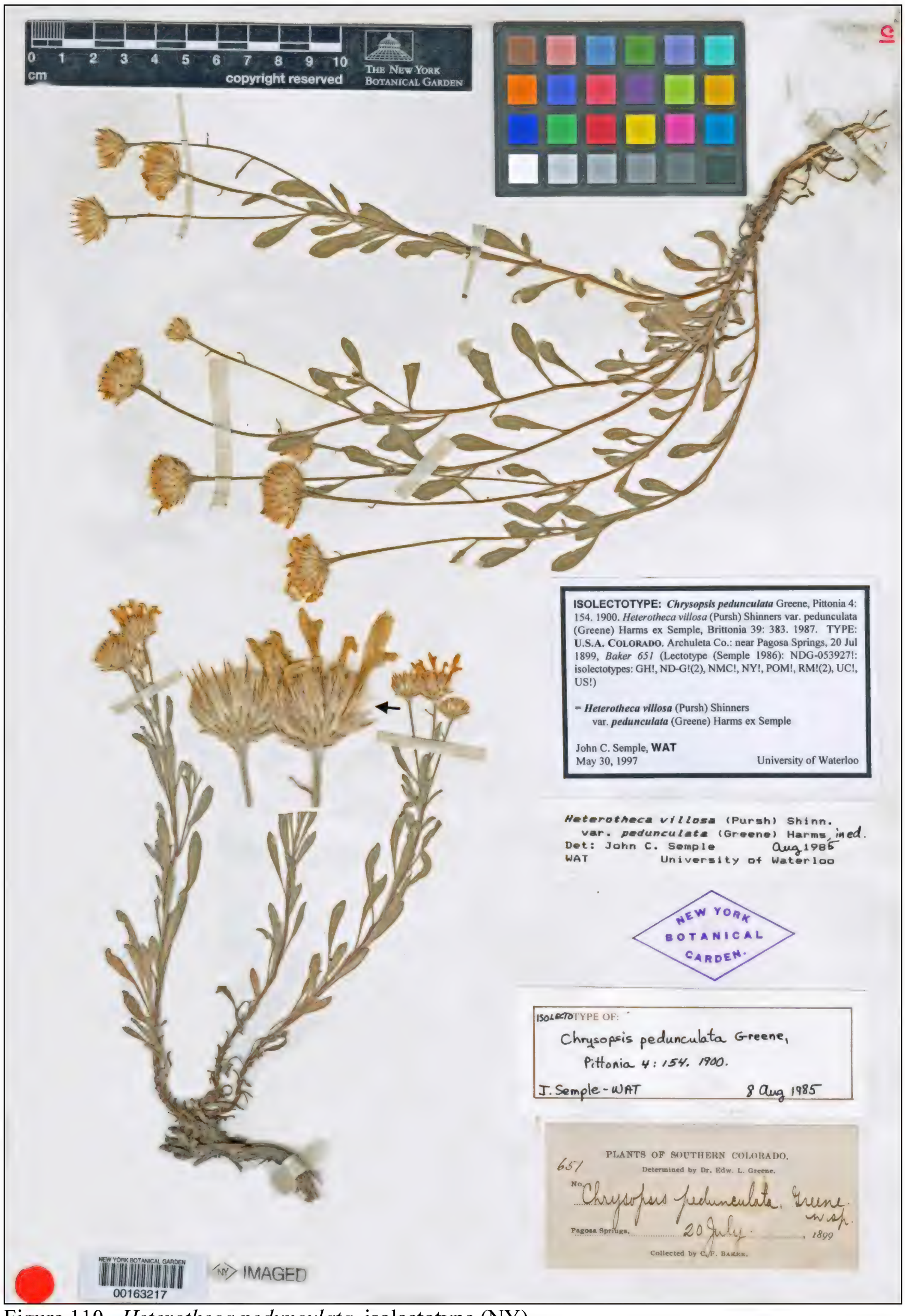


Figure 110. *Heterotheca pedunculata*, isolectotype (NY).

Figure 111. *Heterotheca pedunculata*, Archeluta Co., Colorado. *Harms 2050* (KANU).

Figure 112. *Heterotheca pedunculata*, Archuleta Co., Colorado. *Harms 2053* (KANU).

Figure 113. *Heterotheca pedunculata*, Archuleta Co., Colorado. *Rink 2352* (ASC). Clustered heads is an atypical feature of *H. pedunculata* (perhaps resulting from stem damage?).

Figure 114. *Heterotheca pedunculata,* perhaps with influence of *H. inflata*. Gunnison Co., Colorado, *Baker 794* (RM).

Figure 115. *Heterotheca pedunculata*, Colfax Co., New Mexico. *Legler 10327* (COLO). Perhaps a distinctive variant.

Figure 116. *Heterotheca pedunculata*, Colfax Co., New Mexico. *Legler 10327* (RM).

Figure 117. *Heterotheca pedunculata*, Colfax Co., New Mexico. *Legler 10327* (UNM).

Figure 118. *Heterotheca pedunculata*, Colfax Co., New Mexico. *Harms 19111* (KANU). The label says "Union Co." but "7 mi W of Gladstone" is within adjacent Colfax County, several miles west of the Union County line, at about 6100 feet elevation. Vestiture and relatively long peduncles without capitular bracts place this plant with *H. pedunculata* but the degree of branching and narrow leaves are unusual, perhaps reflecting genetic influence of *H. canescens* or *H. angustifolia*.

Figure 119. *Heterotheca* aff. *pedunculata*, Ouray Co., Colorado. *Wetter 633* (NY). The closely strigose vestiture and long-pedunculate heads without capitular bracts are typical of *H. pedunculata*, but the narrow leaves and congested stems at the base are not. The collector's note that plants were "forming large mats."

Figure 120. *Heterotheca pedunculata*, Montrose Co., Colorado. "Uncompahgre variant" (see text), *Rollins 1599* (NY).

Figure 121. *Heterotheca pedunculata*, Montrose Co., Colorado. "Uncompahgre variant," *Payson 205* (NY).

Figure 122. *Heterotheca pedunculata*, San Juan Co., Utah, La Sal Mts. "Uncompahgre variant," *Franklin 4289* (NY).

Figure 123. *Heterotheca pedunculata*, San Juan Co., Utah, S side of Abajo Peak on Abajo Peak Road, 0.8 road mi below the peak, ca. 10,700 ft, at *Nesom het17-6*. Photos by Nesom, 15 August 2017. These plants are part of the "Uncompahgre variant" population system (see text).

In early phases of this study, I identified plants of *Heterotheca depressa*, *H. hartmanii*, and *H. incensa* as part of a variable *H. pedunculata*. Each of the three, however, proved to be morphologically and geographically discrete and distinct from *H. pedunculata*. *Heterotheca inflata* apparently also is closely related to *H. pedunculata* and *H. orsoensis* probably is most closely related to *H. depressa*. The following key separates these species but there is significant parallel variability and use of the map (Fig. 71) will be central toward understanding concepts of the entities defined here.

25. HETEROTHECA INFLATA Nesom, **sp. nov. TYPE**: **Colorado**. Delta Co.: Gunnison Watershed, Cedar Edge [= Cedaredge], 7000 ft, 24 Jun 1901, *C.F. Baker 241* (holotype: MO!; isotypes: K image!, POM!). *Baker 241* (and also *Baker 103* and *123*) was annotated by E.L. Greene as a new species with the epithet "incana" but the name was never published. A near topotype is *Nesom het17-19* (cited below).

Similar to *Heterotheca hirsutissima* in its spreading stem vestiture and heads without capitular bracts but distinct in its larger heads (involucres 9–16 mm wide) on thicker, longer, bracteate peduncles and its consistently sessile-glandular leaves. *Heterotheca inflata* is further distinguished by its hirsute to hispid-hirsute leaves with arching-ascending hairs, moderately finely hirsute and minutely sessile-glandular phyllaries, and 12–22 ray flowers.

Plants taprooted, not rhizomatous. **Stems** ascending to erect-ascending from the base, 10–45 cm tall, green or purplish, vestiture hirsute to hispid-hirsute, or sometimes hairs spreading below but ascending on distal 1/3, 1- or 2-storied. **Leaves** cauline (basal usually withered by flowering) or basal and cauline, basal sessile, petioloid-attenuate, cauline oblanceolate, subpetiolate, spreading to ascending, often twisted, blades mostly (1–)2–5 cm x (2–)3–12 mm, relatively even-sized up to the peduncles, surfaces strigose-hirsute to loosely strigose, usually prominently sessile-glandular, margins and petioles not prominently ciliate. **Heads** solitary on few-bracteate or leafy-bracteate peduncles (2–)4–10 cm long (or longer when stem unbranched) or sometimes appearing loosely corymboid on long, sometimes stiffly divaricate peduncles, without capitular bracts; involucres (7–)9–16 mm wide; phyllaries sparsely strigose to strigose-hirsute, minutely sessile-glandular, scarious-margined, inner (5–)7–10 mm long. **Ray flowers** mostly 12–22, laminae (1–)2–3 mm wide. Chromosome numbers, $2n$=18 (*Raven 13044*, Delta Co., Colo.; *Semple 8812*, La Plata Co., Colo.), $2n$=36 (*Semple & Heard 7788*, Delta Co., Colo.; *Semple 8815*, San Juan Co., Utah). The epithet ("inflata") alludes to the prominent heads (like balloons) on long, bracteate peduncles.

Flowering May–Sep, lower-elevation populations begin flowering in May and Jun and with a wet summer may produce a new flush of buds and flowers in Aug; desert grassland, salt desert shrub, riparian, juniper-grassland, juniper-Gambel's oak, pinyon-juniper, sagebrush, ponderosa pine, granite outcrops and slopes, sandstone, loess, clay flats, meadows, roadsides and roadbanks; 4500–8000 (–8800) ft.

The geographic range of *Heterotheca inflata* lies within that of *H. pedunculata* but populations of the two apparently are separated ecologically, with *H. inflata* in drier habitats, usually at lower elevations. The two are similar in general aspect (relatively few heads, lack of capitular bracts) but *H. pedunculata* tends to be rhizomatous and has larger heads, eglandular leaves, and leaves and stems (at least distally) strigose with closely appressed hairs, often silvery-sericeous. A hybrid population system may exist along along the crest of the Uncompahgre Plateau (Montrose, Mesa, and Ouray counties, especially abundant in at 7900-9450 feet — see details under *H. pedunculata*, where collection data for these are cited). These plants are consistent in their eglandular, closely strigose leaves; stem vestiture characteristically is antrorse but loosely appressed and usually with an overstory of long, spreading hairs; production of a strongly woody or lignescent taproot is more similar to *H. inflata* than to typical *H. pedunculata*. My personal collections of these have been identified and distributed as *H. pedunculata*, perhaps with influence of *H. inflata*; others were annotated as *H. inflata*.

The diagnosis contrasts *Heterotheca inflata* with *H. hirsutissima* because of their similarity in spreading stem vestiture and lack of capitular bracts, but the evolutionary relationship of *H. inflata* may be closer to *H. pedunculata*.

Additional collections examined. **Colorado**. Delta Co.: Cactus Park, ca 25 air mi WNW of Delta, pinyon/juniper in sandstone canyons, 6340-6400 ft, 8 Aug 2010, *Brummer 1807* (RM); Dominguez Canyon, middle section of trail to Cactus Park Trail junction, ca 20 air mi NNW of Delta, desert grassland and shrubland with scattered pinyon and juniper in wide sandstone canyon, 4950-5700 ft, 25 May 2011, *Brummer 3088* (RM); Gunnison Gulch Trailhead area, NE of Bennetts Basin, ca 18.5 air mi W of Delta, pinyon/juniper woodland on sandstone mesa, 7060-7300 ft, 10 Jun 2011, *Brummer 3793* (RM); Unaweep Canyon, Jacks Canyon Road, near old quarry, above Unaweep Canyon, ca 14.5 air mi SW of Whitewater, in sandstone derived soils on granite outcrop, 7000-7100 ft, 17 May 2012, *Brummer 7662* (RM); mesa above Farmers Canyon, W of Jacks Canyon Road, ca 14 air mi SW of Whitewater, pinyon/juniper woodland, 7360-7520 ft, 17 May 2012, *Brummer 7702* (RM); above Milbern Bench, E of Ninemile Road, ca 3 air mi SW of Whitewater, juniper grassland, 5200-5320 ft, 17 May 2012, *Brummer 7725b* (RM); Oak Mesa, S slopes off BLM road from NE end of Coal Road, at Jay Creek crossing, ca 6.5 air mi NNE of Hotchkiss, meadow area in pinyon/juniper, 7300-7520 ft, 5 Jun 2012, *Brummer 8477* (RM); North Fork Valley, Gunnison National Forest, Hubbard Creek Trail N of Juanita Junction, ca 8.5 air mi NNW of Paonia, along trail in mixed mountain shrub community, 6497-6957 ft, 14 Jun 2012, *Brummer 8718* (RM); Tabeguache Trail or SS Road, just NW of Dominguez Canyon and SE of Gibbler Gulch, ca 25 air mi WNW of Delta, sandstone pavement in ponderosa pine, 7159 ft, 14 Sep 2012, *Brummer 11932* (RM); Horse Mesa, ca 22 3/4 air mi NNW of Delta, sagebrush meadow in pinyon/juniper, 7317 ft, 14 Sep 2012, *Brummer 11970* (RM); Little Dominguez Canyon from Poison Canyon to the bend on the E side of Star Mesa, ca 16.5 air mi WNW of Delta, sandy soil in sparse pinyon/juniper/shrub/rock mix. 5039-5240 ft, 17 Sep 2012, *Brummer 12065* (RM); Youngs Peak and lower intrusive mtn immediately SE, adjacent to Crawford, pinyon-juniper, 6600-7400 ft, 20 May 1997, *Hartman 56661* (RM); ca. 5 mi N of Paeonia, 1785 m, locally common roadside weeds, 2 Jul 1999, *King & Garvey 10956* (BRIT, MO); Hwy 133, 0.2 mi S of jct with Hwy 87 in Paonia, 5650 ft, roadside with *Grindelia*, just into flower (again), few plants, 18 Aug 2017, *Nesom het17-18* (unicate); 3.8 mi N of Cedaredge (Main Street) on Hwy 65 at jct with Ute Trail Road, oak-juniper-pine, 6970 ft, abundant along roadsides with *Grindelia*, 2nd flush of flowering, 18 Aug 2017, *Nesom het17-19* (15 dups); slopes of Grand Mesa, 8000 ft, 21 Jul 1936, *Ramaley 15424* (RM); 13.8 mi NW of Delta on Hwy 50, clay flats, 2 Jun 1958, *Raven 13044* (UC); Landsend, sagebrush, 24 Jun 1938, *Read R-377* (RM); 9.7 km N of Main St., Cedaredge on Colo Hwy 65, stoney (pumice) roadside, juniper-Gambel oak, 8 Sep 1985, *Semple & Heard 7788* (UC). Garfield Co.: 6 mi E of Glenwood Springs, 5900 ft, 21 Jun 1945, *Smith & Harrington 1114* (ASC). Gunnison Co.: Curecanti Natl Rec Area, ca. 1.2 air mi W of Co. Rd 26, ca. 3 air mi S of Blue Mesa Reservoir, ca. 3.9 air mi SE of Sapinero, sagebrush, 7480-8360 ft, 16 Jun 1999, *Arnett 4238* (RM); Roger's, 9000 ft, 14 Aug 1901, *Baker 794* (RM-2 sheets); Soap Creek, dry rocky soil, 7520 ft, 16 Jul 1961, *Hall 554* (BRY); ca. 1.5 air mi NNE of Cimarron, slope down to Gunnison River, S-facing steep slope, 8400-8800 ft, 20 Jun 1997, *Taylor 1674* (RM). La Plata Co.: N of Durango on US Hwy 550, red sandstone slopes by road, 15 Jun 1987, *Semple 8812*, 2n=36 (COLO, MO). Mesa Co.: Grand Junction, 4500 ft, 17 May 1898, *Crandall s.n.* (RM); campsite beside East Creek, 2.2 mi S of jct Hwys 141 and 50, 18 May 1973, *LeDoux et al. 667* (BRY); mesa N of Cave Canyon, ca. 5.5 air mi S of Gateway, pinyon-juniper-sagebrush, 7000 ft, 23 Jun 1994, *Lyon 4941* (RM); 9 mi NE of Gateway, along West Creek, ca. 8 air mi E of Utah border, riparian community of cottonwood and squawbush, loamy gravel, 5400 ft, 18 Jun 1983, *Neese 13669* (BRY, RM); 0.6 mi NW of Colorado River in McDonald Creek drainage, ca. 11 air mi SW of Mack, sandy soil, junipers, 4500 ft, 16 Jun 1983, *Neese & Abbott 13598* (BRY); 1 mi N of Gateway General Store on Hwy 141, area of juniper-sage, 4650 ft, common along roadside, 2nd flush of flowering, 19 Aug 2017, *Nesom het17-29* (3 dups); hills S of Grand Junction, 18 Jun 1926, *Osterhout 6555* (RM); Colorado Natl Monument, among pinyons and junipers, sandy loam, 6500-6700 ft, 24 Jun 1938, *Pennell & Schaeffer 22145* (PH); along State Hwy 141, above East Creek, 4.2 mi W of jct with US Hwy 50, sandy soil at base of large boulders with *Juniperus osteosperma*, 4800 ft, 2 Jun

Figure 124. *Heterotheca inflata*, Delta Co., Colorado, 3.8 mi N of Cedaredge (Main Street) on Hwy 65, at *Nesom het17*. Photo by Nesom, 18 August 2017.

Figure 125. *Heterotheca inflata*, Garfield Co., Colorado, west of Delta on Hwy 92. Photo by Nesom, 18 August 2017.

Figure 126. *Heterotheca inflata*, Delta Co., Colorado. *King & Garvey 10056* (NY).

Figure 127. *Heterotheca inflata*, Delta Co., Colorado. *Siplivinsky 1457* (COLO).

Figure 128. *Heterotheca inflata*, Dolores Co., Colorado. *Bye 1223* (COLO).

Figure 129. *Heterotheca inflata*, La Plata Co., Colorado. *Semple 8812* (COLO).

Figure 130. *Heterotheca inflata*, San Juan Co., Utah. *Windham 90-209* (UT).

1983, *Wilken & Kelly 13969* (BRY). Montezuma Co.: Mesa Verde Natl Park, Wetherill Mesa, 9 Jun [no year], *Erdman 13* (WTU). Montrose Co.: Deer Run, 4700 ft, 11 Jun 1901, *Baker 103* (POM, RM-2 sheets, UC); Black Cañon, 7000 ft, 12 Jun 1901, *Baker 123* (MO, POM, RM-2 sheets, UC-2 sheets); Escalante Creek, ca 17.5 air mi WSW of Delta, pinyon-juniper in sandstone canyon, 5600-6000 ft, 4 Aug 2010, *Brummer 1547* (RM); mesa area W of Linscott Canyon, ca 10 air mi SW of Montrose, pinyon/juniper on sandstone mesa,7380-7400 ft, 4 Aug 2010, *Brummer 1581* (RM); Monitor Mesa, ca 16.5 air mi SW of Delta, pinyon/juniper on sandstone mesa, 6680-7200 ft, 13 Aug 2010, *Brummer 2034* (RM); Freshet Draw, W of Happy Canyon, ca 6 air mi SSW of Montrose, pinyon/juniper forest on sandstone mesa, 6280-6330 ft, 29 May 2011, *Brummer 3315* (RM); hills SE of Cedar Creek, ca 10 air mi SE of Montrose, pinyon/juniper with scattered mountain shrubs, 6580-7800 ft, 21 Jun 2011, *Brummer 4267* (RM); Sawmill Mesa Road, ca 15 air mi SW of Delta, pinyon/juniper woodland with sagebrush and desert grassland openings on sandstone mesa top, 7040 ft, 8 Jul 2011, *Brummer 4840* (RM); Roubideau Creek, above junction with Potter Canyon to 2 trail mi upstream, ca 11 1/4 air mi SW of Delta, riparian area in desert canyon, 5240-5400 ft, 19 May 2012, *Brummer 7811* (RM); mesa SE of Cushman Creek, off of Tabeguache Trail, ca 14.5 air mi ESE of Montrose, in pinyon/juniper, 6900-7200 ft, 2 Jun 2012, *Brummer 8325* (RM); hillsides SW of Waterdog Basin, ca 11.5 air mi SE of Montrose, pinyon/juniper, 7780-8160 ft, 11 Jun 2012, *Brummer 8658* (RM); 7N Mesa, off of Forest Road 525 near The Saddle, ca 16 air mi SW of Delta, sparse pinyon/juniper/rock mix, 6861 ft, 18 Jun 2012, *Brummer 9061* (RM); Sawmill Mesa, NW of Stone Basin, ca 15 air mi SW of Delta, grassy swale in sagebrush, 6270-6300 ft, 25 Aug 2012, *Brummer 11401* (RM); Roubideau Canyon; middle canyon just NW of Camel Back, ca 17 air mi NW of Montrose, low elevation riparian area, 5600-5640 ft, 19 Sep 2012, *Brummer 12097* (RM); near Cerro Summit ca. 200 ft higher, US Hwy 50, 49.4 mi SW of Gunnison and 14.3 mi E of jct US 50 and Colo 90 with US 550 in Montrose, gambel oak, maple in draws, aspen and sagebrush on ridges, 7650-7850 ft, 16 Jun 1968, *Cox et al. 201* (MO); La Sal Creek, 2 mi E of Utah line, abundant in sandy places, 9 Jul 1939, *Cutler 2634* (DS); Coal Canyon, ca. 6.5 mi NE of Nucla, 7000 ft, 31 Aug 1988, *Kass 2796* (BRY); Black Canyon of the Gunnison Natl. Monument, southern rim, ca. 2400 m, locally common, 1 Jul 1999, *King & Garvey 10948* (BRIT, MO); San Miguel Canyon, confluence of San Miguel and Dolores rivers, ca. 6.5 air mi WNW of Uravan on S side of Colo Hwy 141, sandstone ledges, pinyon-juniper, 5300 ft, 9 May 1993, *Lyon 711* (RM); Long Park, Horsethief Spring, ca. 5 air mi NE of Uravan, sandstone, pinyon-juniper, 6250 ft, 26 May 1993, *Lyon 1241* (RM); ca. 20 air mi WNW of Nucla, adjacent to Colo Hwy 90, ca. 2 road mi SW of Paradox, pinyon-juniper and yucca, 6000 ft, 1 Jun 1994, *Moore 1958* (RM); ca. 18 air mi NW of Naturita, ca. 2.5 air mi S of Bedrock, E side of Dolores River Canyon, pinyon-juniper, 5000 ft, 17 Jun 1995, *Moore 5517* (RM); ca. 21 air mi WNW of Naturita along LaSal Creek at the Cliff Dwellers Mine, Co. Rd X4, SE of Colo Hwy 90, 5600 ft, 17 Jun 1995, *Moore 5553* (RM); ca. 13 road mi SW of Montrose on Road 90, NE of Rim Road jct, pinyon-juniper-sage-rabbitbrush, 7500 ft, abundant along roadsides and scattered through woods, 2nd flush of flowering just beginning, 19 Aug 2017, *Nesom het17-20* (5 dups); ca. 12.5 mi SE of Columbine Pass on FS Rd 503 toward Nucla, ca. 4 air mi NE of Nucla, pinyon pine-juniper-Gambel's oak, 6750 ft, common in meadow and openings, 19 Aug 2017, *Nesom het17-25* (2 dups); ca. 16 mi SE of Columbine Pass on FS Rd 503 toward Nucla, ca. 5 mi NE of Nucla, sagebrush-juniper, 6300 ft, abundant along roadside in red, rocky soil, 2nd flush of flowering, 19 Aug 2017, *Nesom het17-26* (4 dups); 1.5 mi W of Nucla on "W 10th Ave" = CC Road = Calamity Road, ca. 1.5 mi E of jct with Hwy 141, sagebrush and scattered juniper, 5550 ft, abundant on roadsides, 2nd flush of flowering, 19 Aug 2017, *Nesom het17-27* (6 dups); 19 mi S of Gateway on Hwy 141, 5 mi S of Mesa Co. line, narrow, steep-walled canyon of the Dolores River, riparian vegetation, 4750 ft, common along roadside, 2nd flush of flowering, 19 Aug 2017, *Nesom het17-28* (4 dups); between Buckeye and LaSal guard stations at jct road to Paradox, ponderosa pine, 5500 ft, 1 Jul 1954, *Sharsmith 4442* (WTU); Hwy 347, ca. 1 mi S of entrance to Black Canyon Natl Mon, pinyon-juniper, ca. 8000 ft, 29 Jun 1984, *Stein & Neill 1823* (RM); Black Canyon of the Gunnison, 3 mi WNW of Dawson's cabin, granite, 6600 ft, 7 Jun 1936, *Rutter 68* (UC); Paradox, dry rocky hills, 5000 ft, 21 Jun 1912, *Walker 148* (DS, RM). Ouray Co.: Billy Creek State Wildlife Area, junction of Brook Creek and Billy Creek, ca 15 1/4 air mi SE of Montrose, salt desert shrub in bottom land, 6857 ft, 13 Sep 2012, *Brummer 11861* (RM); mts E of Colona, open stony slope, 8000 ft, 29 Aug 1920, *Payson 2338* (RM). San Miguel Co.: Disappointment Valley, ca. 13 air mi NE of Dove Creek on Mineral Mtn on Co. Rd K20, pinyon-juniper, 6400-6800 ft, 6 Jun 1995, *Moore 5116* (RM);

Disappointment Valley, ca. 15 air mi NE of Dove Creek Co. Rd 19Q, Dawson Draw, pinyon-juniper, 6100-6700 ft, 21 Jun 1995, *Moore 5854* (RM). **Utah**. Grand Co.: Dolores Triangle, T22 S, R25E, S33, blackbrush community, 1500 m, 15 May 1997, *Atwood 22222* (BRY); La Sal Mts, Dolores Point, ca. 11 mi NE of Mt. Waas, 7520 ft, pinyon-juniper-sagebrush, 25 Aug 1985, *Franklin 2384* (BRY, infl more like *H. pedunculata*); NE of Moab, Negro Bill Canyon, sandstone outcrops, juniper-sage, 4360 ft, 19 May 1986, *Franklin 3146* (RM); SE end of Castle valley, 14.5 mi E of Moab, Gambel oak, sage, pinyon-juniper, 6800 ft, 5 Jun 1986, *Franklin 3430* (BRY); Fisher Valley at mouth of Cottonwood Canyon, E side of Fisher Creek, base of cliff, 5600 ft, 25 May 2004, *Hufford 4229* (WS); slopes above Buckhorn Draw, granitic slopes, juniper and *Purshia*, 4900 ft, 26 May 1994, *Lyon 3439* (RM, mixed collection with *H. polothrix*); Buckhorn Draw, streambed, dry, sandy wash, pinyon-juniper, 4600 ft, 26 May 1994, *Lyon 3495* (RM); Stinking Spring, ca. 6.5 mi up Onion Creek from Hwy 128, 5150 ft, 25 May 1977, *Mikus 543* (BRY); near Moab by the old river bridge, 6 Apr 1988, *Trotter s.n.* (BRY). San Juan Co.: Dodge Point, ca. 8 mi S of Monticello, Allan Farm, 27 Aug 1972, *Allan 216* (BRY); Dugway on E side of Navajo Mtn, ponderosa pine-*Arctostaphylos*, 14 Jul 1971, *Atwood et al. 2978* (BRY); Mile 28 along San Juan River, desert shrub, sandy/rocky soil, 6 May 1997, *Atwood et al. 21860* (BRY); Devil's Canyon campground, 1 Sep 1946, *Cottam 9527* (BRY); Roan Bailey Mesa, red Entrada sandstone, 1900 m, 19 Jun 1985, *Higgins 15813* (BRY); Flat Inn Mesa, sandy soil, 5500 ft, 17 Jul 1939, *Range Survey s.n.* (BRY); along road between Moab and Monticello, ca. 1500 m, 22 Jul 1911, *Rydberg & Garrett 9120* (RM); S of Monticello, meadow, 2100 m, 24 Jul 1911, *Rydberg & Garrett 9144* (RM); 21.2 km NNE of Blanding on US Hwy 163, open ground and fine loess roadcut, 15 Jun 1987, *Semple 8815* (BRY); Cliff Dwellers Pasture, ca. 15 mi WSW of Monticello, rock outcrops and loose soil below head of box canyon, juniper-yucca-manzanita, 7400 ft, 27 Jun 1984, *Tuhy 1531* (BRY); Windwhistle Campground 6 mi W of Hwy 191, desert, 6200 m, 29 May 1996, *Walker s.n.* (UTC image!); Cedar Mesa, N Fork Road Canyon, Cedar Mesa sandstone, sandy soil on floodplain bench near *Populus fremontii*, *Fraxinus anomala*, *Amelanchier utahensis*, 5640 ft, 31 May 1999, *Yeatts 4260* (KHD image!).

26. HETEROTHECA DEPRESSA (Rydb.) Dorn, Vasc. Pl. Wyoming (ed. 1), 295. 1988. *Chrysopsis depressa* Rydb., Mem. New York Bot. Gard. 1: 381. 1900. *Heterotheca villosa* var. *depressa* (Rydb.) Semple, Novon 4: 53. 1994. **TYPE**: **Wyoming**. Teton Co.: Yellowstone National Park, Lower Geyser Basin, 7000 ft, 4 Aug 1897, *P.A. Rydberg* and *E.A. Bessey 5067* (holotype: NY image!; isotypes: NEB image!, NY image!, US image!).

Plants taprooted, not rhizomatous. **Stems** numerous, 12–30 cm, erect to erect-ascending, crowded from a woody caudex, strigose to moderately villous-hirsute with loosely spreading-ascending to irregularly spreading hairs, vestiture essentially 1-storied or with a few longer hairs, eglandular to sparsely and minutely sessile- or stipitate-glandular. **Leaves** cauline (basal not persistent), uncrowded and evenly distributed, oblanceolate, 15–40 x 3–9 mm, proximal subspatulate, spreading to closely ascending, loosely strigose to sparsely moderately hirsute-strigose on both surfaces with ascending hairs, eglandular or sparsely to densely sessile-glandular. **Heads** solitary or in a loose to compact corymboid arrangement, peduncles (0.2–)1–5(–25) cm, without capitular bracts or sometimes with 1–2 lanceolate capitular or subcapitular bracts about as long as the involucre. **Involucres** (5–)7–9 mm wide (pressed); phyllaries elliptic-lanceolate to narrowly obovate-lanceolate, inner (4–)6–7 mm long, sparsely strigose to hirsute-strigose, eglandular to sparsely sessile-glandular, margins scarious and often purple-tinged. **Ray flowers** 8–14. **Chromosome numbers**: $2n$=18 (Teton Co.: *Semple & Zhang 10434*, *10438*), $2n$=36 (Teton Co.: *Semple & Brouillet 7217*); $2n$=36 (Cache Co., Utah: *Windham 91-245*).

Flowering (Jun–)Jul–Aug. Sandy open slopes, sandy bottoms, banks, and terraces of rivers and creeks, gravelly sand bars and gravel flats, river cobblestone, calcareous ridges and outcrops, quartzite, cliffs and ledges, dry rocks, open, rocky slopes and ridges, roadsides, abandoned railway grades, travertine, geyserite, dry soil near hot springs, sagebrush, lodgepole pine burns, subalpine fir, spruce-subalpine fir, limber pine; 5000–9600 ft; Utah, Idaho, Montana (the two Montana collections, see Fig. 132, appear to be adventive along the highway), and Wyoming.

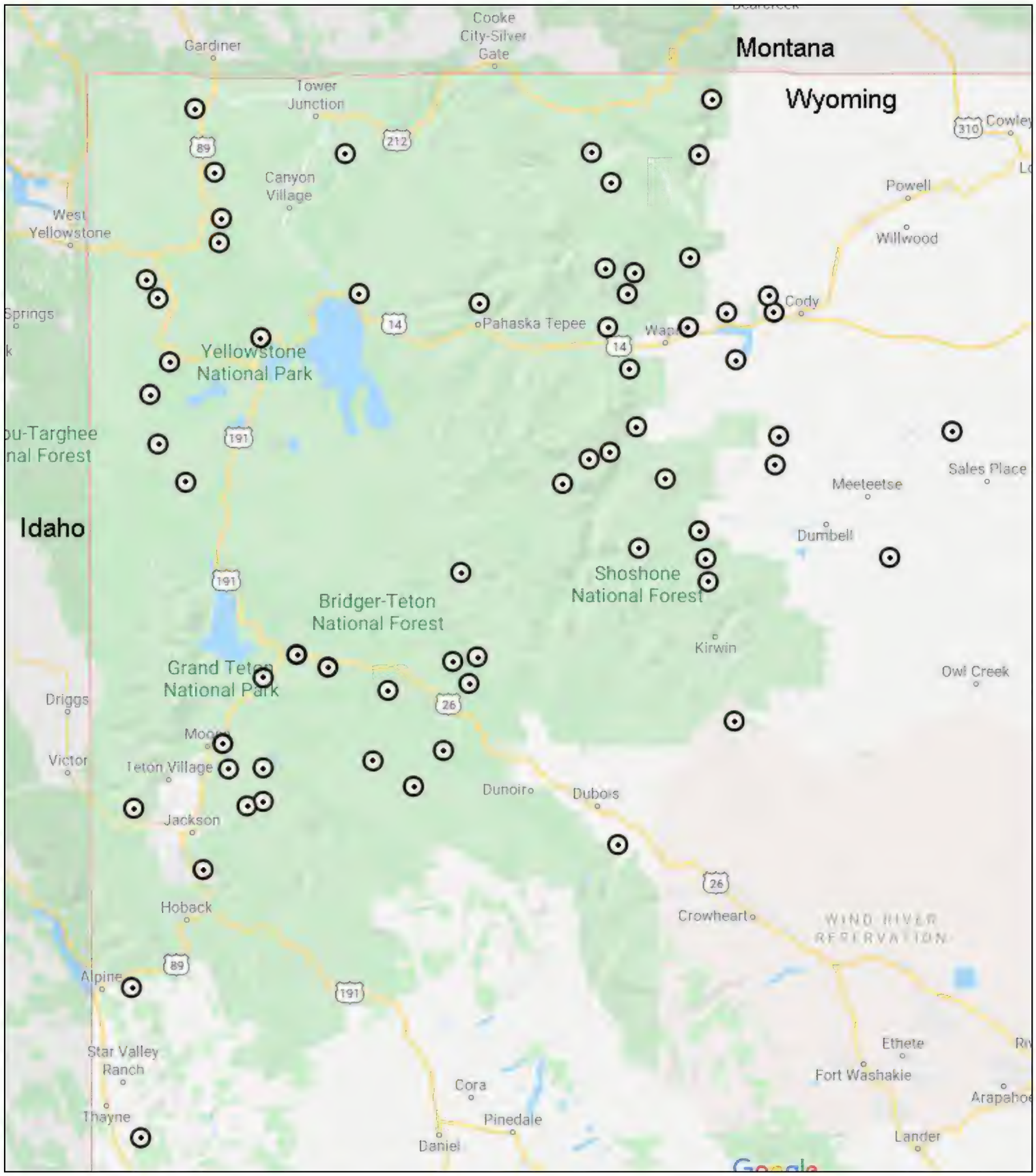


Figure 131. Distribution of *Heterotheca depressa* in Wyoming. The overall distribution (Wyoming, Montana, Idaho, Utah) is shown in Map 11 and Fig. 106.

The type of *Heterotheca depressa* was collected in close vicinity of hot springs and geyser basins in Yellowstone National Park. The caudex branches/proximal portions of the stems sometimes become elongate and rhizome-like (or at least decumbent), resulting in a mat or broad cushion (hence Rydberg's epithet) with crowded leaves. Other plants growing in the travertine and geyserite tend to have the same growth form, e.g., *Blake 10416* (LL), *Blake 10427* (LL), *Blake 10458* (LL), *Jepson 2537* (JEPS), *Sargent s.n.* (BRY), *Thompson 14164* (LL), *Treakle 255* (POM), but others from around the hot springs are erect or intermediate in habit, e.g., *Rose 32388* (CAS) from "rocky slopes, Old

Faithful" and *Van Dyke s.n.* (CAS) from "Mammoth Hot Springs." The erect form is more abundant in the immediate area, and in agreement with Dorn (2001), Evert (2010), and others, it is regarded here as characteristic of the species. In earlier phases of the present study, I identified the erect plants as "*H. pedunculata* N form." In the Yellowstone area, *H. depressa* is sympatric with only *H. hispida* (in Park Co.) and *H. hirsuta*, both of which are immediately distinct in morphology.

Earlier in this study, I identified and annotated collections from Bear River and Franklin cos., Idaho, and Cache Co., Utah, as an undescribed species with the epithet "orsoensis." Further along, it became more evident that their separation from typical *Heterotheca depressa* was essentially arbitrary. Plants from the southern part of the range ("orsoensis") sporadically develop capitular bracts and have glandular leaf surfaces, but similar variation occurs in the region of typical geography, and analogous variation, especially in vestiture, occurs in other species. Perhaps collections will be made in Caribou Co., Idaho, to show a more continuous distribution of *H. depressa*. but as of this date, I have not seen a collection of any *Heterotheca* species from that county.

Collections examined. **Idaho**. Bear Lake Co.: "Blooming Lake" [= Bloomington Lake], 5 Aug 1939, *Davis 1651* (IDS-2, LL); Bear Lake, 6 Aug 1898, *Mulford 327* (MO). Bonneville Co.: South Fork Snake River, T3N R41E S9, cobbly dry floodplain, 5035 ft, 4 Aug 1993, *Merigliano s.n.* (ID). Franklin Co.: 1 mi SE of Cleveland, dry slopes, sagebrush-grass, 26 Jul 1952, *Baker 9532* (ID image!, SRP image!); 5 mi S of Ashton, lava reefs along Snake River, 18 Jul 1945, *Christ 14971* (WS); Bear River Range, 12 mi E of Preston, Upper Cub River drainage, Hillyards Canyon, quartzite (limestone outcrop upslope), open, rocky slope within subalpine fir forest, with *Agastache urticifolia*, *Sedum debile*, *Potentilla glandulosa*, 7700 ft, 18 Aug 1984, *Johnson & Brunsfeld 2237* (CIC image!, ID image!); Bear River Range, ca 0.5 mi W of Gibson Basin, ca 9 mi W of Fish Haven, rocky-gravelly ridgecrest soil, dolomite, with *Pinus flexilis*, *Linanthastrum nuttallii*, *Leucopoa kingii*, *Lomatium graveolens*, 9000 ft, 17 Jul 2002, *Mancuso 2342* (CIC image!, ID image!); Bear River Range, Cache NF, Upper Logan River area, ridge W of Gibson Basin, ca. 8.5 mi W of Fish Haven, SE-facing slope and ridgeline, gravelly soil and ledges on dolomite outcrops, with *Artemisia tridentata*, *Castilleja applegatei*, *Agropyron spicatum*, *Leucopoa kingii*, *Lomatium kingii*, 9000 ft, 17 Jun 1990, *Moseley 1765* (ID image!); Bear River Range, Franklin Basin, N end [label says "Oneida Co." but the loc. apparently is in Franklin Co.], 7800 ft, 24 Jul 1910, *Smith 2275* (RM, UTC image!). Franklin Co.: Franklin Basin, White Canyon, 8300 ft, 30 Jul 1958, *Cottam et al. 15304* (UT); Bear River Range, 12 mi E of Preston, Upper Cub River drainage, Hillyards Canyon, open, rocky slope within subalpine fir forest, quartzite, 7700 ft, 19 Aug 1984, *Johnson & Brunsfeld 2237* (ID); Bear River Range, ridge ca 0.7 mi N of Cub Peak, ca 11 air mi W of St. Charles, Cache National Forest, in open, rocky, dry, forb and low shrub-dominated community, quartzite, 8850 ft, 19 Jul 1990, *Mancuso 279* (ID); Bear River Range, ca. 9 mi W of Fish Haven, ca. 0.5 mi W of Gibson Basin, rocky-gravelly ridgecrest soil, dolomite, 9000 ft, 17 Jul 2002, *Mancuso 2342* (ID); Bear River Range, ca. 8.5 mi W of Fish Haven, upper Logan River area, ridge W of Gibson Basin, SE-facing slope and ridgeline, dolomite, gravelly soil and ledges on outcrops, 9000 ft, 17 Jul 1990, *Moseley 1765* (ID). Fremont Co.: St. Anthony city park, on rocks, 13 Jul 1937, *Cronquist 685* (IDS image!, UC); cliffs above Henry's Fork of Snake River at Lower Falls, 5500 ft, 13 Jul 1939, *Cronquist 1653* (MO, RM); Stage Station, Snake River, 3 Aug 1885, *Letterman 24* (MO); Fremont County Burning Project, lava reefs, sagebrush, 5000 ft, 20 Jul 1948, *Lingenfelter 557* (RM); Targhee Natl Forest, Island Park Plateau, road to rocks, St. Anthony, 4 Jul 1901, *Merrill & Wilcox 794* (RM); Fremont County Burning Area (T10N R40E), rocky reefs, sagebrush, 5500 ft, 20 Jul 1934, *Pechanec 34-45* (RM); Targhee Natl Forest, Robinson Creek just N of Horseshoe Lake, Site 65, Island Park Geothermal Study Area, dry thin soil in crevices of boulders (southerly exposure), *Pinus flexilis*, 1870 m, 27 Aug 1977, *Whitehead 1063* (IDS image!); Targhee Natl Forest, 3 km E of US Hwy 191 on Anderson Mill Canyon Road, Site 79, Island Park Geothermal Study Area, dry thin soil in crevices of boulders (southerly exposure), *Pinus flexilis*, 1830 m, 10 Sep 1977, *Whitehead 1175* (IDS image!); Targhee Natl Forest, dry rocky area between Sardorus Hill Road and Snow Creek Canyon, Site 130, Island Park Geothermal Study Area, dry thin soil in crevices of boulders (southerly exposure), *Pinus flexilis*, 1710 m, 23 Jul 1978, *Whitehead 1503* (IDS image!).

Figure 132. *Heterotheca depressa*, Broadwater Co., Montana, in a ruderal habitat and perhaps adventive at the northernmost known extent of its range. Typical morphology. *Booth c82* (KANU).

Figure 133. *Heterotheca depressa*, Fremont Co., Idaho. *Whitehead 1503* (IDS).

Figure 134. *Heterotheca depressa*, Fremont Co., Idaho. *Whitehead 1175* (IDS).

Figure 135. *Heterotheca depressa*, Fremont Co., Idaho. *Christ & Ward 14971* (NY).

Figure 136. *Heterotheca depressa*, Franklin Co., Idaho. *Moseley 1765* (ID).

Figure 137. *Heterotheca depressa*, Bear Lake Co., Idaho. *Mancuso 279* (ID).

Figure 138. *Heterotheca depressa*, Cache Co., Utah. *Snell 1049* (WTU).

Montana. Broadwater Co.: 2 mi S of Townsend, scattered plants in disturbed area along roadside, 20 Aug 1950, *Booth c82* (KANU image!, WTU). Park Co.: 5 mi W of Livingston, sandy road cut, 5 Aug 1941, Booth C82 (ID). **Utah**. Cache Co.: Tony Grove Lake, 8300 ft, 15 Aug 1938, *Cronquist 1088* (IDS image!, MO); Wasatch-Cache Natl Forest, vicinity of Tony Grove lake, ca. 0.75 mi N of parking area along Trail to Naomi Peak, on sandy soil over rocky ledges, ca. 8500 ft, 9 Jun 1997, *Leidolf 2171* (BRIT); head of Tony Grove Basin, rocky slopes and ledges, 8100 ft, 18 Aug 1938, *Maguire 16107* (WTU); Wasach-Cache Natl. Forest, Bear River Range, Franklin Basin, 1.5 air mi W of Logan River, ridge NW of Crescent Lake, head of Crescent Lake Canyon, SE-facing slope, Swan Peak Quartzite, 9000 ft, 18 Aug 1981, *Neely 666* (UTC image!); South Tony Grove Lake on Tony Grove Smithfield Trail, 9500 ft, 26 Aug 1927, *Price 62* (RM); Tony Grove Lake, 9600 ft, 26 Aug 1927, *Price s.n.* (ID image!, WTU); Cache Natl Forest, trail to Mount Naomi, 1/2 mi N of Tony Grove Lake, spruce-subalpine fir, ca. 8700 ft, 12 Sep 1980, *Shaw 2645* (BRY); 0.5 mi N end of Tony Grove Lake, dry rocky places, 8200 ft, 6 Aug 1938, *Snell 1049* (PH, WTU-2 sheets); NW of Tony Grove Lake, Bear River Range, ca. 1.3 km S of the summit of Mt. Magog, thin soil over limestone, E-facing slope, montane conifer forest, 8625 ft, 20 Aug 1991, *Windham 91-245,* **n=18II** (MO). **Wyoming**. Many collections (RM! and others) from northern Lincoln Co., Park Co., and Teton Co.

27. HETEROTHECA INCENSA Nesom, **sp. nov.** **TYPE**: **Utah**. Daggett Co.: Flaming Gorge National Recreation Area, ca 1 air mi W of Flaming Gorge Dam, Cart Creek drainage into Flaming Gorge, dry pinyon-juniper uplands with clay soils, sandstone bluffs, and steep slopes, 6160-6600 ft, 23 Jun 1994, *C.H. Refsdal 1133* (holotype: RM, Fig. 143).

Distinct in its combination of caespitose habit, equably leafy stems, hirsute and 1-storied stem vestiture, leaves sessile-glandular adaxially, heads on leafy peduncles (short branches), lack of capitular bracts, and ovate-lanceolate to triangular phyllaries with scarious margins.

Plants taprooted, without rhizomes or elongate caudex branches. **Stems** 8–30(–50) cm, crowded from the caudex apex, erect to ascending-erect, simple or few-branched usually at midstem or above, often purplish proximally, vestiture hirsute with spreading to sharply upward-arching hairs to loosely strigose (1-storied) with loosely ascending hairs, often with a mix of spreading and loosely ascending hairs, usually all spreading on the distal half, eglandular; axillary buds (as small leaf tufts) present and usually conspicuous. **Leaves** cauline (basal withered by flowering), proximal attenuate to a petiole-like base, becoming epetiolate distally with truncate to rounded base and relatively even-sized to near the heads, oblong- to elliptic-lanceolate to oblanceolate or narrowly oblong-oblanceolate, ascending, largest at midstem, midcauline 8–40 x 2–6(–8) mm, narrowly attenuate to a petiolar region, petioles most pronounced proximally, becoming epetiolate distally, surfaces sparsely to moderately strigose-hirsute to hirsute with arching hairs, consistently sessile-glandular adaxially, glandular or eglandular abaxially, margins not ciliate or with cilia thicker-based but only slightly longer than other hairs. **Heads** solitary or in a loosely paniculate or loosely corymboid arrangement, peduncles leafy-bracteate and indistinct or sometimes ebracteate and 5–35 cm long, capitular bracts absent. **Involucres** 7–10 mm wide (pressed), phyllaries narrowly elliptic-lanceolate to ovate-lanceolate, strigose-hirsute to short hirsute-villous, eglandular or distally glandular, inner (5–)6–8 mm long, margins scarious-rimmed. **Ray flowers** 10–17, laminae 1.5–2.0 mm wide. **Chromosome numbers**, 2*n*=18 (*Semple 5764*, *5768*, Moffat Co.), 2*n*=36 (*Windham 96-154*, Daggett Co.).

Flowering May–Aug(–Sep). Sandstone outcrops and crevices, canyon bottoms, sandy floodplains and flats, roadside, roadbanks, clay soil, sagebrush, juniper, pinyon-juniper, pinyon-juniper with ponderosa pine, ponderosa pine, lodgepole pine; (4500–)5200–8400(–9000) ft.

Heterotheca incensa is abundant in the Flaming Gorge area (whence the epithet) of Daggett Co., Utah, extending into adjacent Sweetwater Co., Wyoming, Uintah Co., and northwestern Colorado, and southward through Utah. In its northern range, it occurs sympatrically with *H. utahensis*, although the latter apparently is less common in the area — *H. utahensis* is distinct in its taller, more strictly erect, and thicker stems, consistently hirsute stem vestiture of longer and more

distinctly 2-storied hairs, larger and more oblong, often epetiolate leaves, and heads characteristically in a more compactly corymboid arrangement.

Additional collections examined. Colorado. Garfield Co.: East Fork of Middle Stewart Gulch, 2 2/3 miles S of Rio Blanco County line, SE-facing slope, loam, with *Artemisia* and grasses, 2438 m,12 Jul 1982, *Popp & Waters 82-370* (MESA). Mesa Co.: Ca. 5 air mi NE of Gateway, dry wash and adjacent hillsides with pinyon and juniper, 5500 ft, 16 May 1994, *Lyon 3150* (RM); near Colorado River opposite Fruita, limestone knoll, 5100-5300 ft, 24 Jun 1938, *Pennell & Schaeffer 22164* (PH); Gateway Palisade Natural Area, N of Gateway between Hwy 141 and Dolores River, The Palisade, flat mesa summit in rocky, gritty soil, 7045 ft, 21 Jun 2007, *Yeatts 5495* (COLO, KHD); Gateway Palisade Natural Area N of Gateway between Hwy 141 and Dolores River, E of Mesa Co road 4.2 on W side of the Palisade, base of N-facing Wingate cliff of penisula fin extending W from main Palisade ridge, in rock crevices and on narrow ledges in thin soil just below vertical pouroff, 6173 ft, 30 Aug 2010, *Yeatts 5953* (BRY, COLO, KHD); Gateway Palisade Natural Area, N of Gateway between Hwy 141 and Dolores River, 1.15 mi SE of Palisade summit, graveLly drainage bank and low bench in pine-juniper, 4840 ft, 10 Oct 2015, *Yeatts 6349* (KHD). Moffat Co.: 1 mi E of Sunbeam, xeric hillside facing Yampa River to the N, 28 Jul 1933, *Hanna 1324* (MO); Sunbeam, S of Yampa River, sagebrush slope, 28 Jul 1933, *Hermann 5346* (MO); ca. 31.5 air mi WNW of Maybell, northern toe slopes of Douglas Mtns, 1.3 road mi S of jct (Greystone) with Co Rd 10 on Douglas Mountain Blvd (Co Rd 60), E side of rd, crevices of sandstone bedrock, pinyon-juniper-sagebrush-ponderosa pine, 6913 ft, 10 Jun 2013, *Johnson 2402* (BRY, OBI); Dinosaur Natl Monument, 0.5 mi SSW of Hackings Springs, *Pinus edulis*, *Juniperus osteosperma*, and *Artemisia tridentata*, 8000 ft, 28 Jun 1988, *Kelley 88-81* (COLO); 10.5 km W Craig on US 40, sagebrush, 3 Oct 1982, *Lane 2985* (COLO); Blue Mtn, Round Top, E-facing slope, among limestone ledges, 8600 ft, 30 Jun 1960, *MacLeod 24A* (COLO); Douglas Mtn, Whisky Spring house area, N slope, 7500 ft, 11 July 1960, *MacLeod 180A* (COLO); 6 mi SW of Greystone, Douglas Mtn, near Lower Whisky Spring at Whisky Springs Ranch, NE-facing slope with cheatgrass and wild rose bushes, 7525 ft, 30 Jul 1964, *MacLeod 281* (COLO); 6 mi SW of Greystone, Douglas Mtn, at Whisky Springs Ranch, NE-facing slope with sagebrush and serviceberry, 7520 ft, 4 Jul 1964, *MacLeod 283* (COLO); Dinosaur Natl Monument, Bull Canyon, 0.8 mi SE of Yampa River, pinyon-juniper, 5840 ft, 2 Sep 1988, *Naumann 290* (COLO); Dinosaur Natl Monument, Indian Water Canyon, ca 1 mi S of East Cactus Flat, S of Old Chuckwagon Road, gravels and cracks of sandstone of drainage with *Pinus*, *Juniperus*, and *Artemisia*, 6300 ft, 18 May 1987, *Neely 4049* (COLO, RM); Dinosaur Natl Monument, E. Fork Sand Canyon, W of the Billiard Table, sandy soils of gentle N exposure in wash with *Sarcobatus*, *Artemisia tridentata*, *Clematis*, and *Senecio*, 5500 ft, 30 May 1987, *Neely 4149* (COLO, NY); Dinosaur Natl Monument, Pool Canyon, 0.2 mi E of Utah border, canyon bottom with *Pinus*, *Juniperus*, *Rhus*, and *Symphoricarpos*, 6160 ft, 1 Jun 1987, *O'Kane 2996* (COLO, RM); Dinosaur Natl Monument, first major draw E of Big Joe Draw, N of Starvation Valley, bottom of draw with *Pinus* and *Juniperus*, 6660 ft, 25 Jun 1987, *O'Kane 3147* (COLO, RM); Pat's Hole, near confluence of Greene and Yampa rivers, dry sandy soil, 4500 ft, 8 Jul 1945, *Porter 3635* (MO, RM, SMU, TEX, WTU); Dinosaur Natl Monument, Hells Canyon, sandy flats, 21 Jun 1948, *Rodeck 4439* (COLO, WTU); E of Elk Springs on Hwy 40, juniper-sage, 30 Aug 1981, *Semple 5764*, **2*n*=18** (COLO-2 sheets, NY); E of Elk Springs on Hwy 40, 30 Aug 1981, *Semple 5768*, **2*n*=18** (ASU, COLO, MO, UTC); Dinosaur Natl Monument, ca. 2 mi E of Dinosaur, near jct of US Hwy 40 and park road to Echo Canyon, 5934 ft, 30 Jul 2009, *Urbatsch 10372* (LSU); SE slope of Cold Spring Mountain on primitive road to Little Joe Basin between Bull Canyon and Irish Canyon, gypsum hills and alkaline flats, 27 Jun 1965, *Weber & Salamun 12662* (COLO). Rio Blanco Co.: Buford, 7200 ft, 23 Aug 1910, *Duce 382* (COLO); Aldrich Lake, meadow, 22 Jul 1937, *Johnson s.n.* (COLO); 3 mi N of jct of No Name Ridge and Piceance Creek, frequent on sandy loam of W facing slope, 7775 ft, 30 Jun 1982, *O'Kane & Riefler 82-498* (COLO); Meeker, 9 Aug 1910, *Robbins 7156* (COLO); ca 17 air mi E of Meeker, Flat Tops/White River Plateau, ridge between Big Beaver and Fawn Creeks, rocky, gentle S-facing slope, 8500 ft, 14 Aug 1990, *Vanderhorst 1723* (COLO); 4 mi W of Rangely on the N side of White River, white sandstone cuesta, rock crevices 5250 ft, 15 Jun 1978, *Weber & Wingate* 15398 (COLO, CS). **Utah.** Daggett Co.: Hideout Canyon Campground, S exposure W in Spring Canyon, 6000 ft, 22 Aug 1956, *Cottam 14536* (UT); Green River, 6100 ft, 11 Jun 1959, *Flowers et al. 216* (UT); head of Cart Creek, Ashley Forest, 5500 ft, 29 Jun

1929, *Garrett s.n.* (BRY); Uintah Mts, along Spring Creek on road from Manila to Vernal, xeric hillside, 11 Jul 1933, *Hanna 1269* (MO); Uintah Mts, Greens Lakes, open yellow pine, 9000 ft, 11 Jul 1933, *Hanna 1292* (MO); N slope Uinta Mountains, Ashley Natl Forest, Dripping Spring, ca 2 air mi SE of Dutch John, pinyon-juniper with some ponderosa pine and stream bottoms, 6000-6200 ft, 24 May 1994, *Hartman 45327* (MO, RM); Sheep Creek Gorge, dry sagebrush slope, 7300 ft, 11 Jul 1933, *Hermann 4743* (MO); Green Lakes, yellow pine-sagebrush slope, 7500 ft, 11 Jul 1933, *Hermann 4801* (MO); Uintah Mts, S shore of East Green Lake, mountain meadow, 7400 ft, 11 Jul 1933, *Hermann 15155* (RM); Carter Creek, 8000 ft, 4 Jul 1944, *Jensen s.n.* (WS, WTU; dups at IDS and UC are *H. elata*); 2 mi E of Dutch John, dry slopes at Dripping Springs Campground, 4 Jun 1986, *McNeilus s.n.* (TENN); Doud Mtn overlook, ca. 4 mi N of Rte 44, dry slopes, 2 Jul 1986, *McNeilus s.n.* (TENN); near bottom of Sears Canyon, Taylors Flat, 5750 ft, 15 Jun 1978, *Neese 5659* (BRY); N slope Uinta Mountains, Flaming Gorge Natl Recreation Area, ca 2 air mi W of Red Canyon Visitor Center along Carter Creek, SE side of Carter Creek drainage into Flaming Gorge, willows dominant, 6000-6400 ft, 23 Jun 1994, *Refsdal 1149* (RM); N slope Uinta Mountains, Flaming Gorge National Recreation Area, ca 2 air mi S of Dutch John on the E side of the Green River, S of Flaming Gorge Dam, pinyon-juniper woodlands, some riparian areas, and W-facing red sandstone cliffs, 5600 ft, 11 Jul 1994, *Refsdal 1652* (RM); Flaming Gorge Natl Recreation Area, Red Canyon Visitor Center, ca 10 air mi SE of Manila, ridgetop with sagebrush and juniper on sandstone-gravelly soil, 7400 ft, 11 Jul 1994, *Refsdal 1661* (RM); Three Corners, ca. 20 air mi ENE of Dutch John, 8400-8520 ft, 5 Jul 1995, *Refsdal 4935* (BRY); Clay Basin, ca 7.5 air mi NE of Dutch John., S aspect, spring, dark humus soils, gravelly sagebrush, 6760-6840 ft, 5 Jul 1995, *Refsdal 4965* (BRY, RM); N slope Uinta Mountains, Ashley Natl Forest, Burnt Creek, ca 10.8 air mi SSE of Manila, S side of Utah Hwy 44, dry upland, ponderosa pine, red soils with clay, 7900-8000 ft, 21 Aug 1995, *Refsdal 7552* (RM); N slope Uinta Moutains, Ashley Natl Forest, East Fork Eagle Creek, ca 9.6 air mi SE of Manila, 1.4 mi W of Red Canyon Road on both sides of Forest Road 529, upland, lodgepole pine, 7700-8080 ft, 2 Sep 1995, *Refsdal 7808* (RM); N slope Uinta Moutains, Ashley Natl Forest, Carter Creek, ca 8.1 air mi S of Manila on N side of Utah Hwy 44, upland, ponderosa pine, scattered juniper, mostly clay soils,7200-7300 ft, 2 Sep 1995, *Refsdal 7857* and *Refsdal 7868* (RM); 4.2 km N of Dutch John, US-191, pinyon pine-juniper scrub, 16 Sep 1987, *Semple & Chimielewski 8870* (BRY, MO); 18.2 km S of Dutch John, US-191, lodgepole pine woods, 16 Sep 1987, *Semple & Chimielewski 8871* (BRY, MO); ca. 7 mi due SE of Manila, N flank of Boars Tusk Ridge, 6300 ft, 27 Jun 1978, *Welsh & Moore 18697* (BRY, RM); ESE of Dutch John near Green River on rim of Swallow Canyon, ca. 6.39 km SSE of Whisky Spring, N-facing slope with *Artemisia*, *Pinus*, and *Juniperus*, rocky sandstone soil, 5950 ft, 22 May 1996, *Windham 96-154*, *n*=18 (UT). Emery Co.: Cedar Mountain SW of Recreation Area, 30 Jul 1975, *Albee 692* (UT); Temple Mountain, dry slopes, 31 May 1962, *Allman s.n.* (BRY); Desolation Canyon, Green River, valley bottom, 4800 ft, 10 May 1999, *Atwood 24448* (NY); San Raphael Swell-East Ferron, dry wash, 5500 ft, 6 Jun 1932, *Cottam 5269* (UT); NW of Huntington along Hwy 31, Manti-La Sal Natl Forest, narrow canyon with Huntington Creek on S side, ca. 6000 ft, 31 Jul 2004, *Estes et al. 6616* (APSC); 4.6 mi S of Calf Creek Canyon on road to I-70, barren knolls with scattered juniper and *Ephedra*, 5200 ft, 31 May 1981, *Hreha 285* (UT); San Rafael Swell, head of Black Dragon Canyon, mixed desert shrub, Navajo sandstone, 4600 ft, 24 May 1989, *Kass 2984* (NY); Calf Springs Wash, sandy canyon bottom, 11 May 1940, *Maguire 18330* (NY); Range Creek Canyon, S end of Cherry Meadow in floodplain of Lighthouse Canyon, E of Range Creek, piney covered knoll in sagebrush flat, 5680 ft, 16 Jun 2006, *RCC 2006-30* (UT); Range Creek Canyon, ca. 0.9 mi S of jct Turtle Canyon and Range Creek roads, BLM, sandy loam with *Tamarix* and *Populus*, 4660 ft, 29 Jun 2007, *RC 2007-27* (UT); CC Price River, 21 mi SE of Huntington, pinyon-juniper, 7600 ft, 22 Aug 1977, *Welsh 16168* (NY). Garfield Co.: Calf Canyon, 15 mi S of Boulder, sandy bottom, 3500 ft, 7 Aug 1952, *Cottam 13444* (UT); ca. 1/2-3/4 mi N of Escalante River, along Sand Creek, 5280 ft, 31 May 1989, *Hodgson 5621* (DES); 1 mi S of Hell's Backbone Bridge, Navajo Sandstone outcrops along road, 5 Aug 1981, *Hreha 322* (UT); end of Long Neck Mesa between Deer Creek and Slickrock Canyon, E of Boulder, sandy soil pocket in slickrock, 6350 ft, 19 Sep 2010, *Licher 2966* (ASC); 5 mi N of Escalante, along Lower Pine Creek at the Lower Box Trailhead, riparian on Navajo sand, ca. 6400 ft, 15 Jun 2011, *Madsen 5683* (KANU); Cons Hole at the head of South Fork Oak Creek, Navajo Sandstone, ponderosa pine/manzanita community, 7700 ft, 12 Jun 2012, *Madsen 6007* (KANU); Escalante River, between Death Hollow and Sand Canyon, scattered pinyon pine and juniper, sandy soils above

riverbed, 15 May 1984, *Neely 1954* (COLO). Grand Co.: Moab, 4000 ft, 8 May 1933, *Cottam 5573* (UT); NE of Moab, ca. 2 mi E of Hwy 163 along Hwy 128, Navajo Sandstone, along road, 14 May 1981, *Hreha 166* (UT); ca. 40 mi NE of Moab, Rio Mesa Center, Utah Bottoms along Dolores River, top of mesa on E side of campground, rocky, sandy soil, 1302 m, 22 May 2016, *Kilbane 11* (UT); Porcupine Ridge, Sand Flat Road, red sandy soil, 30 Jun 1967, *Pederson 108* (UT); Grand River crossing, opposite Moab, 1200 m, 30 Jun 1911, *Rydberg & Garrett 8355* (UT); bank of Colorado River at Dewey, sandy soil among rocks, 4500 ft, 23 May 1953, *Vickery 243* (UT); S side of Colorado River ca. 3/4 mi below the Dewey bridge, talus slope, 4100 ft, 23 May 1953, *Vickery 298* (UT); 3.5 km N of Dewey Bridge, along fence line on N-facing hillside near State Rte 128, near dry river bed, 4254 ft, 21 May 1994, *Woodford s.n.* (UT). Kane Co.: Ca. 7 mi N of Kanab and 1.6 mi E of US Hwy 189, Kanab Creek NE of road to John R Flat within Best Friends Animal Sanctuary, banks of sandy terrace above active floodplain, openings in *Populus-Salix*, 5200 ft, 14 Aug 2008, *Fertig 24255* (UT); N of Kanab, White Cliffs, Best Friends Animal Sanctuary, base of cliffs and lower terrace at confluence of Three Lakes Canyon and Kanab Creek, white sandy soil over Navajo Sandstone bedrock on W- and S-facing slope and terrace, pinyon pine-juniper, 5235 ft, 2 Jun 2011, *Fertig 26536* (ASC); Glen Canyon NRA, ca. 60 mi down Hole-in-the-Rock Road from Escalante, juniper, 4285 ft, 20 May 2003, *Hill 96* (ASC); Grand Staircase Escalante Natl Monument, beach above Escalante River, S side ca. 2.5 mi S of Boulder Creek confluence, sandy wash bottom at base of sandstone cliff, 5150 ft, 16 Sep 2004, *Licher 909* (ASC); 15 mi NW of Orderville, left fork of headwaters of Virgin River, open places on dry slopes around yellow pine, 6600 ft, 15 Jun 1940, *Maguire 18858* (NY). San Juan Co.: Ca. 45 km S of Moab, sandy desert slopes overlooking Hook and Ladder Gulch to the south, 1800 m, 6 Sep 1987, *Cronquist 12077* (UT); from Moab, S on Hwy 191 to Road 131 (Needles Overlook Rd), roadsides, mixed grassland and shrub, sand, 1790 m, 28 Sep 2013, *Johnson 47* (UT). Sevier Co.: Ca. 10 mi due W of Emery on Old Woma Plateau, aspen comm, silty loam soil, 8230 ft, 17 Jul 1980, *Neese & White 9202* (NY). Uintah Co.: Brush Creek near Vernal, dry, rocky hillsides, 8000 ft, 15 Sep 1936, *Andrews & Noble s.n.* (WTU); Elk Horn Ranger Station, rocky soil, sagebrush, 8000 ft, 27 Jul 1928, *Christensen C-4* (RM); 25 mi N of Vernal, lower aspen belt, S slopes, 7000 ft, 27 Jun 1935, *Cottam 6017* (UT); Dinosaur Natl Monument, Split Mountain Gorge Campground, sandy flood plains, 1600 m, 23 Jun 1948, *Dever & Wolf 5093* (COLO); Vernal-Manila hwy, roadside, 21 Aug 1938, *Garrett 7526* (UT); along Vernal-Manila road N of Vernal, 7400 ft, 4 Sep 1935, *Graham 10186* (MO); ca. 10 mi S of Bonanza on Utah Uwy 45, common on sandy soil, 5600 ft, 25 Jul 1965, *Holmgren 2264* (ID, KANU, NCSC, NY); ca. 50 mi SE of Ouray, near Flat Rock Mesa, sandstone outcrop with pockets of reddish soil, pinyon-juniper, 7200 ft, 30 Jun 1980, *Hreha UB-14* (UT); Dry Fork Canyon, ca. 18 mi N of Maeser, *Juniper-Stipa-Amelanchier*, stony slopes, 7200 ft, 22 Jun 1979, *Neese et al. 7815* (RM); top of Blue Mtn, head of Stuntz Draw, crevices of sandstone bedrock in mesic drainage bottom, 7680 ft, 7 Jul 1982, *Neese 11890* (BRY); between K Ranch and Jensen, 18 Jun 1925, *Osterhout 6409* (RM); ca 17 air mi SE of Dutch John, 4.9 mi W of Colorado on both sides of Crouse Creek Road, steep creek side, *Acer*, 6150-6200 ft, 3 Aug 1994, *Refsdal 2452* (RM); ca 19 air mi SE of Dutch John, 6.3 mi SW of the Green River on Crouse Creek Road at the head of Crouse Canyon, flats at the head of the canyon, big sagebrush, juniper, and *Salix* in stream, 6350 ft, 3 Aug 1994, *Refsdal 2476* (RM); Browns Park, Sears Canyon, ca 12.5 air mi SE of Dutch John, red sandy soils, sandstone cliffs, juniper/pinyon pine, cottonwood., 6200-6420 ft, 31 Jul 1995, *Refsdal 6342* (RM); 16 km S of Daggett Co., 27 km N of Vernon intersect. with US Hwy 40 on US Hwy 191, sandstone outcrop with juniper, 16 Sep 1987, *Semple & Chmielewski 8873* (BRY, MO); ca. 5.8 mi NE of Jensen, Green River Campground, between road and Green River or along the edge of the river, 1500 m, 29 Jul 2009, *Urbatsch 10397* (LSU); along US Hwy 40, ca. 16 air mi SE of jct with US Hwy 191, roadside, 1668 m, 29 Jul 2009, *Urbatsch 10403* (LSU); Flynn's Point, Diamond Mtn, NE of Vernal, 7300 ft, 25 Jun 1980, *Williams 80-141-1* (RSA); North-South Canyon ca. 1 mi E of jct of roads to Split Mountain Gorge and Dinosaur Natl Monument Hqs., 22 Jun 1948, *Wolf & Dever 5063* (COLO). Wayne Co.: Dixie Natl Forest, Fish Creek Cove [ca. 2.5 mi NW of Grover, toward Teasdale], 38 13.98' N, 111 24.93' W, base of Navajo Sandstone cliffs on sand in an open ponderosa pine community, 7200 ft, 12 Aug 2004, *Madsen & Merkley 1964* (BRY, ID, UNM); ca. 2.3 mi S of Grover on Hwy 12 toward Boulder, ca. 0.5 mi S of Dixie Natl Forest boundary (within the NF), area of pinyon pine-juniper-ponderosa pine, locally abundant at base of roadside cut through white Navajo sandstone, E side of road, 7850 ft, 15 August 2017, *Nesom het17-1* (BRIT + 6 dups); 3.1 mi S of Grover on Hwy 12 toward Boulder, ca. 1.3 mi

S of Dixie Natl Forest boundary (within the NF), ca. 0.5 mi N of jct with Happy Valley Road, area of ponderosa pine with scattered juniper and small douglas fir, scattered but abundant in sand among basalt boulders, high white Navajo sandstone cliffs to immediate east, E side of road, 8100 ft, 15 August 2017, *Nesom het17-2* (BRIT + 7 dups); Utah Hwy 12, ca. 5 km by road S of Grover, 7900 ft, open ponderosa pine slopes, one plant seen in bud, 16 Jun 1987, *Semple 8822* (BRY); Utah Hwy 12, ca. 5 km by road S of Grover, 7900 ft, 18 Aug 1987, *Semple 8897* (BRY). **Wyoming**. Sweetwater Co.: Red Creek Basin, rocky clay slope with *Juniperus osteosperma*, 6700 ft, 3 Jul 1999, *Dorn 8012* (RM); US Hwy 191, 8.9 km NE of Utah state line, roadside, 28 Aug 1995, *Semple & Zhang 10440* (BRIT); NE slopes and draws of Richards Mtn, ca. 2 air mi NW of Richards Gap, ca. 37 air mi SSW of Rock Springs, sandy draw, 6850-7500 ft, 5 Jul 1996, *Ward 1994* (RM); Washakie Basin, from Cooper Ridge to Salt Creek, E of the confluence of Pretty Water and Salt Wells creeks, ca. 21 air mi SSE to Rock Springs, sandy rocky slopes, 6705-6880 ft, 5 Jul 1996, *Ward 2140* (RM).

Figure 139. *Heterotheca incensa*, Wayne Co., Utah (site of *Nesom het17-1*). Abundant plants along Hwy 12 in loose sand directly derived from Navajo Sandstone. Photo by Nesom, 15 August 2017.

Figure 140. *Heterotheca incensa*, Wayne Co., Utah, 2.3 mi S of Grover on Hwy 12 toward Boulder, at *Nesom het17-1*. Photo by Nesom, 15 August 2017.

Figure 141. *Heterotheca incensa*, Wayne Co., Utah, near locality of *Nesom het17-1*. Scattered plants in sandy soil of ponderosa pine woods. Photo by Nesom, 15 August 2017.

Figure 142. *Heterotheca incensa*, Wayne Co., Utah, near locality for *Nesom het17-1*. *Semple 8822* (BRY). Early season (mid-June) plant, before upper branching and inflorescence development.

Figure 143. *Heterotheca incensa*, Daggett Co., Utah. *Refsdal 1133* (RM). Holotype.

Figure 144. *Heterotheca incensa*, Daggett Co., Utah. *Windham 96-154* (UT).

Figure 145. *Heterotheca incensa*, Daggett Co., Utah. *Cottam 14536* (UT).

Figure 146. *Heterotheca incensa*, Daggett Co., Utah. *McNeilus s.n.* (TENN).

Figure 147. *Heterotheca incensa*, Uintah Co., Utah. *Holmgren 2264* (KANU). Stiff, many-branched stems and relatively small, spreading leaves — a distinctive form needing further study, also occurring in Grand Co.

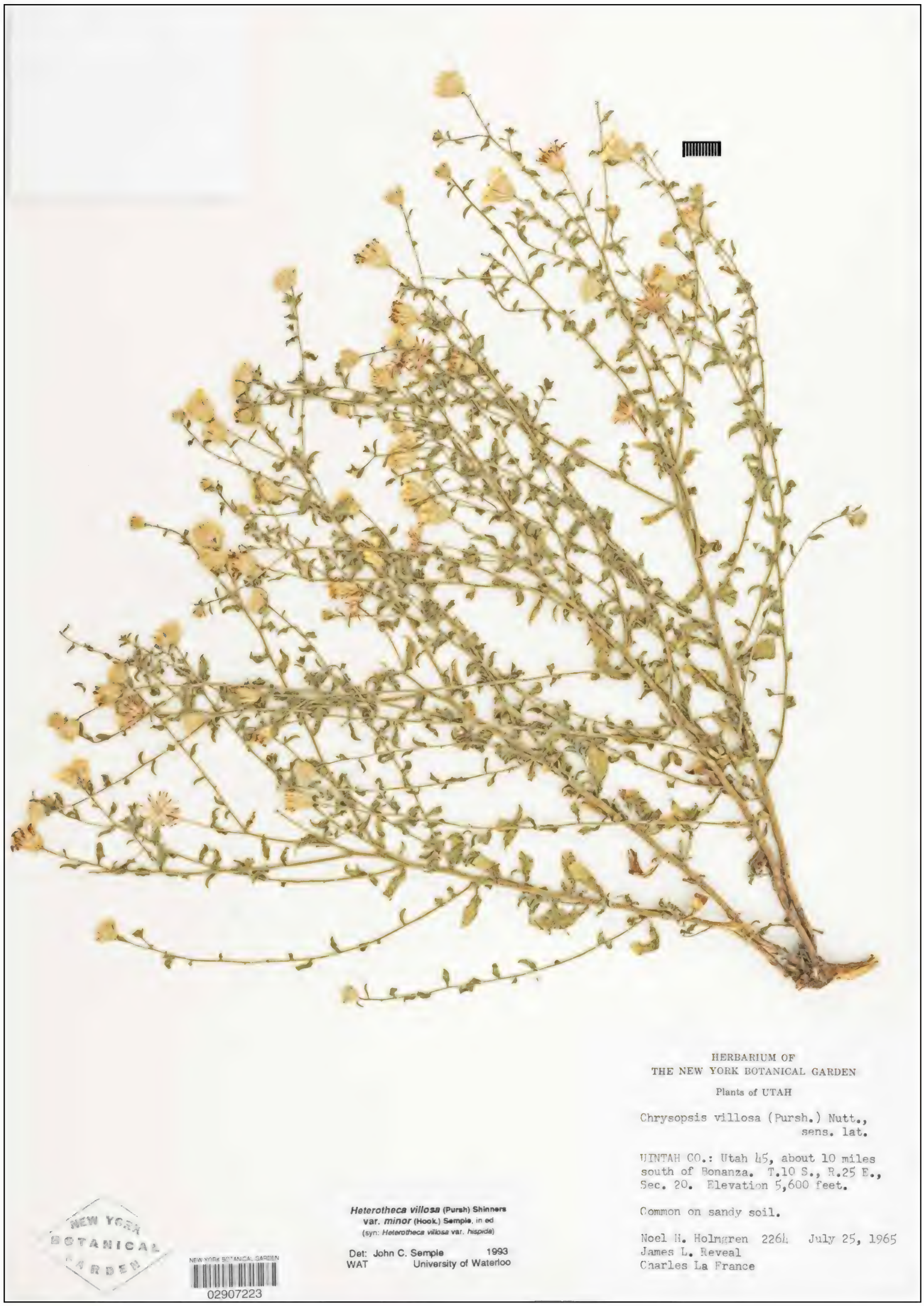


Figure 148. *Heterotheca incensa*, Uintah Co., Utah. *Holmgren 2264* (KANU).

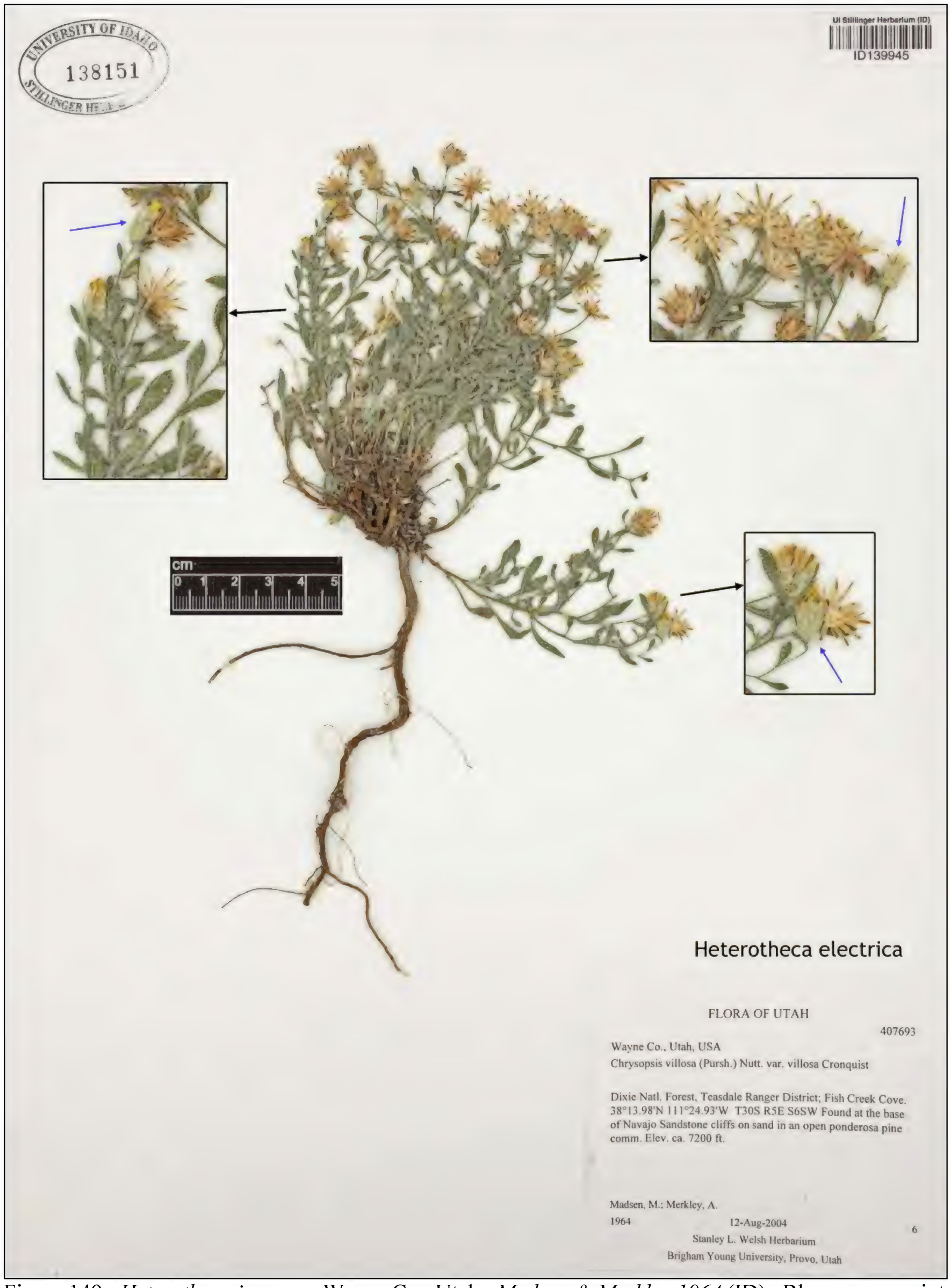


Figure 149. *Heterotheca incensa*. Wayne Co., Utah. *Madsen & Merkley 1964* (ID). Blue arrows point to heads in flower, very small and few-flowered, perhaps due to drought; vestiture hispid-hirsute. The population apparently was consistent in this feature (see duplicate in Fig. 149). Collection is from near Grover, in the vicinity of typical plants.

Figure 150. *Heterotheca incensa.* Wayne Co., Utah. *Madsen & Merkley 1964* (BRY).

28. HETEROTHECA POSTPETRINIS Nesom, **sp. nov. TYPE**: **Utah**. Grand Co.: Pritchett Canyon, 1200 m, 3 Jul 1911, *P.A. Rydberg and A.O. Garrett 8517* (holotype: NY-Fig. 153; isotypes: US-Fig. 155; UT-Fig. 154).

Distinct in its combination of reduced habit, slender and lax, stems unbranched or few-branched near the apex, spatulate-obovate, petiolate cauline leaves, and small, few-flowered, solitary heads subtended by a capitular bract.

Stems slender, probably trailing or reclining, unbranched or branched only in the caudex region and distalmost portion, 14–20 cm long, sparsely hirsute. **Leaves** cauline, basal not persistent or not present, largest at midstem or above, ascending, elliptic-oblanceolate to oblanceolate-obovate or spatulate-obovate, basally attenuate to a narrow petiolar region, with a rounded to obtuse-rounded apex, proximal small and becoming larger distally, largest at ca. midstem, 12–16 mm long, blades 3–5 mm wide, even-sized from midstem up to the involucres, surfaces and margins hirsute, marginal cilia of petiole slightly longer, minutely glandular adaxially. **Heads** solitary, subtended by a capitular bract or bracts similar to the distal cauline leaves. **Involucres** 4.5–6 mm wide (pressed); phyllaries in 3–4 graduate series, narrowly oblong-lanceolate with prominently white-scarious-rimmed margins, inner 6–8 mm long. **Ray flowers** ca. 8–10. Known only from the type collection.

The hirsute vestiture and white-margined phyllaries of *Heterotheca postpetrinis* are similar to *H. incensa*, which grows abundantly in relatively close-by localities. *Heterotheca hirsuta* also occurs in the area, though apparently more rarely. The lax habit and very small heads subtended by capitular bracts of *H. postpetrinus* are like those of the central Coloradoan *H. paniculata*.

The epithet alludes to the locality of *Heterotheca postpetrinis* in Pritchett Canyon, which forms the southeastern border of the Behind The Rocks Wilderness Study Area, immediately south of Moab. Pritchett Canyon (Fig. 152) is essentially east- to west-trending, descending from its upper portion at about 1400 meters to the river at 1200 meters — the label elevation of 1200 meters (ca. 3900 feet) puts the collection locality at the very base of the canyon. The lax stems suggest that the plants are pendent from the sandstone walls of the canyon.

Figure 151. Behind The Rocks Wilderness Study Area, looking east to the La Sal Mountains. Pritchett Canyon forms the southeastern boundary of the WSA. BLM photo.

Figure 152. Pritchett Canyon, Grand Co., Utah, type locality of *Heterotheca postpetrinis*. The town of Moab is about 3 miles northeast of the locality. See Map 16 and Fig. 210 for a map in larger context.

Figure 153. *Heterotheca postpetrinis*, holotype (NY).

Figure 154. *Heterotheca postpetrinis*, isotype (UT).

Figure 155. *Heterotheca postpetrinis*, isotype (US).

29. HETEROTHECA HARTMANII Nesom, **sp. nov. TYPE**: **Wyoming**. Carbon Co.: Sierra Madre, Red Mountain, T14N R85W S31,32, dry mountainside amongst rocks, 10,100 ft, 27 Jul 1988, *N. Kastning 792* (holotype: RM!, Fig. 156).

Similar to *Heterotheca pedunculata* in its antrorsely oriented (mostly strigose) stem vestiture, oblanceolate leaves, and loosely clustered, pedunculate heads but distinct in its geography (north-central Colorado and adjacent Carbon Co., Wyoming), strongly taprooted habit, production of capitular bracts, and narrower phyllaries.

Plants perennial, from a woody taproot. **Stems** 12–45 cm, crowded from the caudex apex, ascending, vestiture loosely strigose, less commonly spreading-ascending to nearly puberulent (perhaps reflecting gene flow from *H. hirsutissima*), eglandular. **Leaves** cauline (basal withered by flowering), ascending, equably distributed, mostly oblanceolate to oblong-oblanceolate or elliptic-oblanceolate, mostly without a distinct petiolar region (except in the largest), largest at midstem or above, midcauline 15–45 x 3–9(–15) mm, axillary tufts of small leaves often evident, surfaces moderately hirsute-villous with arching hairs, both surfaces eglandular. **Heads** few in a loose corymb or loose panicle, peduncles 3–20(–45) mm; prominent capitular bracts usually present, narrowly lanceolate to oblanceolate, shorter to longer than the involucre; involucres 7–11 mm wide, phyllaries narrowly lanceolate, inner 6–8 mm long, sparsely strigose-hirsute to hirsute-villous, eglandular. **Ray flowers** 12–18, laminae 1.2–2.0 mm wide. **Chromosome number**, 2*n*=36 (*Semple 5773*, Routt Co., Colorado).

Flowering (Jun–)Jul–Aug(–Sep). Spruce, spruce-fir, aspen, lodgepole pine, sagebrush, Gambel's oak, pinyon-juniper, meadows, roadsides, cliffs, ridges, talus, rocky hillsides, volcanic outcrops, roadsides; (6900–)8200–10,100 ft. For Dr. Ronald L. Hartman, 1945-2018, who knew while he was still with us that this species would be named for him.

Heterotheca hartmanii is remarkably distinct, especially because of the prominent capitular bracts. It might be confused with *H. pumila* because of their elevational overlap, but the two occur in different habitats and there is no indication that they hybridize. *Heterotheca hirsuta* also is sympatric with *H. hartmanii* and produces capitular bracts, but it differs in vestiture. The discrete geographic range of *H. hartmanii* also supports its standing as an evolutionarily coherent entity.

Heterotheca hartmanii is compared with *H. pedunculata* in the diagnosis, but unlike the ovate-lanceolate phyllaries of *H. pedunculata, H. incensa*, and *H. depressa*, those of *H. hartmanii* are linear-lanceolate, more like those of *H. hirsutissima*. The latter is sympatric with *H. hartmanii* and gene flow apparently occurs where they overlap in elevation (at the lower range of *H. hartmanii*). Examples of probable hybrids or introgressants are *Read 96* (Eagle Co.), *Hartman 73380* (Jackson Co.), and *Nelson 55418* (Routt Co.).

Figure 156. *Heterotheca hartmanii*. Carbon Co., Wyoming. Holotype (RM).

Figure 157. *Heterotheca hartmanii*. Routt Co., Colorado. *Randolph 67* (COLO).

Figure 158. *Heterotheca hartmanii*. Jackson Co., Colorado. *Hartman 70421* (COLO).

Figure 159. *Heterotheca hartmanii*. Garfield Co., Colorado. *Vanderhorst 4416* (BRY).

Collections examined. **Colorado**. Eagle Co.: Gore Range, Big Horn Creek area, FS Trail 2013, ca. 4 air mi E of Vail, 8600-10,600 ft, 13 Jul 2000, *Holt 2151* (BRIT, RM); Sawatch Range, W slope of Continental Divide, Missouri Lakes Trail, ca. 16 air mi S of Avon, spruce-fir/lodgepole pine, 10,200-11,200 ft, 15 Jul 2000, *Holt 2272* (BRIT); Lime Park, 9500 ft, 2 Aug 1916, *Keefe 146* (RM); White River Natl Forest, cliffs uphill from Taylor Creek, ca. 2 air mi ENE of Christine State Wildlife Area and ca. 5 air mi ENE of Basalt, sandstone cliffs and loose slopes with scattered pinyon-juniper and mixed shrubs, 7400-7800 ft, 20 Jun 2010, *Kirkpatrick 1726* (RM); Gore Range, White River Natl. Forest, Eagles Nest Wilderness, Deluge Lake Trail, ca. 7 air mi NNW of Vail Pass, rocky aspen hillsides, 8800-10,200 ft, 2 Aug 2010, *Kirkpatrick 3738* (RM); Sawatch Range, White River Natl Forest, Holy Cross Wilderness, Eagle Lake Trail to Halfmoon Lake, between Eagle and Avalanche peaks along Lime Creek, ca. 18 air mi SSE of Eagle, subalpine riparian corridor, seeps, and scree slopes, 10,100-10,400 ft, 21 Jul 2011, *Kirkpatrick 7708* (RM); Flat Tops/White River Plateau, ca. 18 mi NNE of Eagle, dry hills above Colorado River, pinyon-juniper, 6900 ft, 15 Jul 1991, *Vanderhorst 3338* (RM). Garfield Co.: Uintah Basin, S slope of S rim, head of East Salt Creek, 7500 ft, 16 Jun 1935, *Graham 9704* (UC); ca 4 air mi NW of New Castle, Flat Tops/White River Plateau, Main Elk Creek, E exposure and ridge top, red shale and white sandstone, juniper and oak, 6250 ft, 23 May 1990, *Hartman & Vanderhorst 24520* (COLO); E of Coffee Pot Springs, White River Plateau, rim of Deep Creek Canyon, limestone outcrop, 10100 ft, 29 July 1963, *Miller 54* (COLO); White River Plateau, cutoff to Grizzly Creek Road from Coffee Pot Road, 1/2 mi NW Crne Park, 10,500 ft, 30 Jul 1963, *Miller 295* (COLO); ca 12 air mi N of Glenwood Springs, Flat Tops/White River Plateau, headwaters of Grizzly Creek, meadows and rocks around lake, with *Dugaldia*, *Salix*, clumps of *Abies*, and *Picea*, 10,700 ft, 22 Jul 1990,*Vanderhorst 1212* (KANU); ca 12 mi NE of Glenwood Springs, Flat Tops/White River Plateau: Deep Creek Overlook, top edge of north-facing cliffs and talus slopes above canyon, patchs of *Pinus flexilis* and *Pseudotsuga menziesii*, and unforested rock, 10,000 ft, 23 Jul 1990, *Vanderhorst 1307* (KANU, COLO); Flat Tops/White River Plateau, Grizzly Creek, ca. 4 air mi E of Glenwood Springs, canyon bottom with cottonwood, Douglas fir, spruce, and dogwood, 6000-6200 ft, 24 Aug 1990, *Vanderhorst 1913* (KANU, RM); Flat Tops/White River Plateau, N rim of Deep Creek Canyon around Balixburg Spring, ca. 14 air mi NE of Glenwood Springs, limestone rimrock with limber pine, Douglas fir, and *Selaginella*, 9400 ft, 23 Jul 1991, *Vanderhorst 3510* (COLO); ca 13 air mi N of Glenwood Springs, Flat Tops/White River Plateau, limestone ridge above Bison Lake, exposed limestone with pockets of poorly drained soil, northern exposure, with scattered spruce,11,000 ft, 6 Aug 1991, *Vanderhorst 3868* (KANU); ca 17 air mi NNW of Glenwood Springs, Flat Tops/White River Plateau, Flat Tops Wilderness, Blair Mountain, limestone rimrock, E exposure with ferns, columbine, and willows, 11,200 ft, 24 Aug 1991, *Vanderhorst 4416* (BRY). Jackson Co.: Park Range, Rainbow Lake Trail, ca. 17 mi WSW of Walden, spruce forest, 8800-8900 ft, 7 Aug 2000, *Hartman 69393* (RM); Park Range Newcomb Park Trail, 0.5-2.5 trail mi W of trailhead (to granitic domes and Newcomb Creek, angling NW), 20-21 air mi SW of Walden, meadows and woodland, pond edges, 8800-8900 ft, 17 Aug 2000, *Hartman 70021* (RM); Medicine Bow Mts, Forest Rd 895 at private land and W to North Platte River, then NE 1.5 air mi, ca. 6-7 air mi N of Cowdrey, 7800-8500 ft, 9 Sep 2000, *Hartman 70421* (COLO); Park Range, Lake Percy and Round Lake, around lakes, 10,130 ft, 28 Aug 2001, *Hartman 74030* (RM); Park Range, ca. 2 air mi N of Red Elephant Mtn, spruce-fir, 9250 ft, Aug 1988, *Kastning 1212* (RM); Park Range, ca. 6.5 air mi SSE of Mt. Ethel, sagebrush grassland, 8750 ft, 18 Aug 1988, *Kastning 1315* (RM); Park Range, ca. 16 air mi W of Walden, dry meadows by lodgepole pine forest, 8850 ft, 3 Sep 1988, *Kastning 1375* (RM); Park Range, ca. 18 air mi WSW of Walden, Norris Creek, Livingston Park area, mixed lodgepole pine and aspen stands, 8925 ft, 15 Aug 1989, *Kastning 2643* (RM); Grizzle Creek Ranger Station pasture, sagebrush, 8500 ft, 5 Aug 1930, *Kutzleb K129* (RM); Park Range, Lake Percy and along creek below, ca. 1/4 mi E of the Continental Divide, ca. 4 air mi NW of Rabbit Ears Peak, 26-27 air mi SW of Walden, open slope with scattered willows, 9400-10,060 ft, 17 Aug 2000, *Nelson 51929* (RM); Park Range, below Rabbit Ears Peak on N and E sides, ca. 27 air mi SW of Walden, roadside and along logging roads, 9800-10,100 ft, Aug 2000, *Nelson 52032* (RM); Park Range, along Continental Divide above Manzanares Lake, ca. 26 air mi W of Cowdrey, ca. 30.5 air mi NW of Walden, stony ridge with scattered conifers, 9900-10,350 ft, 1 Aug 2001, *Nelson 55147* (RM); Rabbit Ears Range, along Continental Divide ca. 0.5-1 air mi NW of Chimney Rock, ca. 8 air mi ESE of Muddy Pass, ca. 27.5 air mi SSW of Walden, volcanic outcrop, 9480-9800 ft, 20 Aug 2001, *Nelson 55918* (RM); Hog Park Ranger Station pasture, 8500 ft, 13 Aug 1923, *Rose 121* (RM); Medicine Bow Mts, Colorado State Forest, East

Sand Hills Natural Area, ca. 10 mi E of Walden, W-facing sand dunes with *Artemisia*, 8200-8400 ft, 1 Jul 2001, *Nunn 2365* (BRIT); Park Range, near jct of FS Roads 600 and 689, ca. 0.5 mi N of Big Creek Lake, ca. 22 air mi NW of Walden, large clearing in lodgepole pine forest, 8900 ft, 6 Aug 1989, *Snow 5265* (RM). Moffat Co.: Danforth Hills, Rte 40, SW of Cross Mtn, along draw, sagebrush, 6500-6600 ft, 30 Jun 1938, *Pennell & Schaeffer 22471* (PH). Rio Blanco Co.: vicinity of Aldrich Lake, meadow, 22 Jul 1937, *Ramaley & Johnson 719* (RM); Flat Tops/White River Plateau, Yellow Jacket Pass, ca. 12 air mi NE of Meeker, W-facing slopes above pass, Gambel oak, 7500-8400 ft, 9 Jul 1990, *Vanderhorst 881* (RM); ca. 17 air mi E of Meeker, Flat Tops/White River Plateau, ridge between Big Beaver and Fawn Creeks, rocky, gentle S-facing slope, 8500 ft, 14 Aug 1990, *Vanderhorst 1723* (COLO); ca. 19 mi E of Dinosaur, sandstone outcrops, disturbed salt desert shrub comm., silty sandy clay soil, 10 Aug 1979, *Welsh 320* (BRY). Routt Co.: Park Range, Mt. Zirkel Wilderness, along trail to Gold Creek Lake, near Wilderness boundary, open bank along trail, 8800 ft, 6 Aug 1988, *Flock 2019* (RM); Steamboat Springs, open, stony flats, 22 Jul 1903, *Goodding 1655* (PH-2, RM); Park Range, Middle Fork Elk River, 21 air mi WNW of Walden, spruce-fir, 9000 ft, 21 Jul 1989, *Kastning 2406* (RM); Park Range, ca. 15.5 air mi N of Steamboat Springs, dry meadow, 8170 ft, 27 Aug 1989, *Kastning 2710* (RM); 18 mi NW of Steamboat Springs, Day Creek Ranch, meadows in open aspen-conifer, 8500 ft, 3 Aug 1991, *Keil 22485* (OBI); 5 mi W of Grand Co. line on Hwy 40, Rabbit Ear Pass, pine-Douglas fir, roadside, 9426 ft, 3 Aug 1982, *Luckow 958* (OBI); Park Range, along Service Creek, ca. 4 air mi above the Yampa River, ca. 15.5 air mi SSE of Steamboat Springs, meadow, 8400 ft, 3 Aug 1989, *Nelson 17602* (BRIT, RM); Elkhead Mts, N of Dry Fork Elkhead Creek, ca. 1 air mi SW of Elkhead, ca. 10 air mi N of Hayden, stony sagebrush hills, 6920-7040 ft, 29 Jun 2000, *Nelson 50118* (RM); Park Range, along a tributary of Tennessee Creek E and below Shield Mtn, 6.5-7 air mi NW of Columbine, sandy-rocky knoll with aspen and chokecherry, 8000-8300 ft, 7 Aug 2000, *Nelson 51483* (RM); Park Range, head of Harrison Creek, ca. 2 air mi E of Walton Peak, ca. 3 air mi SW of Rabbit Ears Pass, lodgepole pine on volcanic substrate, 9760-9800 ft, 24 Jul 2001, *Nelson 54545* (RM); Park Range, Walton Peak and vicinity, 4-5 air mi SW of Rabbit Ears Pass, stony ridge on volcanic substrate, 9920-10,560 ft, 24 Jul 2001, *Nelson 54475* (RM); Park Range, N end of Crane Park just above Middle Fork Little Snake River, ca. 6.5 air mi NNE of Columbine, sagebrush, 8240-8360 ft, 31 Jul 2001, *Nelson 55009* (RM); Park Range, at head of Middle Fork Little Snake River and along the Continental Divide, ca. 1-2 air mi ENE of Big Red Park, ca. 8-9 air mi ENE of Columbine, stony ridge with scattered conifers, 9120-10,360 ft, 1 Aug 2001, *Nelson 55116* (RM); Park Range, along old logging road S and E above Rock Creek, 1.5-2.5 air mi ENE of Long Park, 15-16 air mi SE of Yampa, roadside and adjacent lodgepole pine forest, 8800-8900 ft, 8 Aug 2001, *Nelson 55375* (RM); Park Range, along Forest Rd 443 and Trail 1164 between Three Island Creek and S Fork Elk River, ca. 19.5 air mi NNE of Steamboat Springs, roadside in old logged area, 8400-9000 ft, 21 Aug 2001, *Nelson 56021* (RM); Park Range, along Forest Rd 443 and Trail 1164 between Three Island Creek and S Fork Elk River, ca. 19.5 air mi NNE of Steamboat Springs, along trail and in adjacent moist, open spruce-fir-aspen forest, 8400-9000 ft, 21 Aug 2001, *Nelson 56097* (RM); Park Range, along Forest Rd 441 to Floyd Peak above Reed Creek, 5-6 air mi E of Clark, along road through mixed conifer forest, 8900-9200 ft, 22 Aug 2001, *Nelson 56142* (RM); Conger Mesa just N of McCoy, moss-covered rock outcrop, 7700 ft, 7 Jul 1984, *Randolph 67* (COLO); US Hwy 40 SE of Steamboat Springs, foothills 1.5 mi W of Routt Natl Forest boundary, 31 Aug 1981, *Semple 5773*, **2n=36** (MO); Park Range, along Mad Creek Trail, *Quercus gambelii*, *Pinus*, 7600 ft, 3 Aug 1989, *Snow 4799* (RM); Park Range, Gold Creek drainage, near Mt. Zirkel Wilderness boundary, ca. 21 air mi NE of Steamboat Springs, aspen grove, 8500 ft, 10 Aug 1989, *Snow 5706* (RM); open ridge above Micah Lake, 8500 ft, 26 Jul 1926, *Towne 17* (RM); Routt Natl Forest, 28 mi N of Soda Springs, vicinity of Seedhouse Campground, along N Fork Elk River, 8000 ft, 15 Jul 1951, *Weber 6708* (WTU). **Wyoming**. Carbon Co.: Sierra Madre, ca. 4 air mi SSW of Blackhall Mtn, along Encampment River, spruce-fir forest, 8450 ft, 28 Jul 1988, *Kastning 863* (RM) and *Kastning 873* (RM); ca. 10 km N of Wyo Hwy 70, Forest Rd 801 by Forest Rd 801.18, open aspen-pine woods, 9916 ft, 25 Aug 1995, *Semple & Zhang* 10416 (MO).

Several collections, apparently made in close proximity, of near-typical *Heterotheca hartmanii* seem out of range. **Wyoming**. Albany Co.: Laramie Range, N of Laramie ca. 6 mi S of Hwy 34 on Sybille Rd, occasional near roadside on slope, 27 Jun 1991, *Keil 21876* (OBI); Laramie Mts, Medicine

Bow Natl Forest, sandy alpine prairie by I-80, ca. 8600 ft, 1 Sep 1976, *Kral 58965* (MO); Laramie, small, open clumps on loamy sunny slopes, 18 Jun 1913, *Macbride 2478* (RM).

Variants (x *H. hirsutissima* ?). **Colorado**. Eagle Co.: Derby Mesa, N of mill, 8000 ft, 21 Aug 1925, *Read 96* [x *H. hirsutissima* ?] (RM). Jackson Co.: Medicine Bow Mts, Forest Rd 204, 0.7 road mi SE of Forest Service boundary, ca. 1 air mi from Kings Canyon, 8511 ft, 3 Aug 2001, *Hartman 73380* [x *H. hirsutissima* ?] (BRIT, RM); Medicine Bow Mts, Forest Rd 889, 0.1 road mi E of Colo Hwy 127, sagebrush, 8700-8800 ft, 6 Aug 2001, *Hartman 73567* [x *H. hirsutissima* ?] (RM); Medicine Bow Mts, County Rd 8A, 1 mi from Co. Rd 8, then SE on hogback to gap, sagebrush, 8400-8600 ft, 6 Aug 2001, *Hartman 73702* [x *H. hirsutissima* ?] (RM). Routt Co.: Park Range, along Horse Creek to Rock Creek and the ridge to the N, 1.5-2 air mi E of Long Park, 15-16 air mi SE of Yampa, sagebrush, 8550-8880 ft, 8 Aug 2001, *Nelson 55418* [x *H. hirsutissima* ?] (RM).

30. HETEROTHECA HIRSUTISSIMA (Greene) Nesom, **comb. nov.** *Chrysopsis hirsutissima* Greene, Pittonia 4: 154. 1900. **LECTOTYPE** (Semple 1996): **Colorado**. Archuleta Co.: Arboles, 5 Jun 1899, *C.F. Baker 650* (NDG 53929 image!; isolectotypes: E, F, G fragment, GH, K, MO, NDG 53920, NDG 53921, NY, POM-2 sheets!, RM-2 sheets!, UC!, US). Images! of all types.

Semple (1996, p. 126-127) noted that "Some of the type material is close to or covarietal with var. *pedunculata*; thus the type population may have included hybrids between var. *minor* and var. *pedunculata*." It is not clear to me, however, what features led Semple to this conclusion, because all plants and branches on all the type sheets (excluding the G fragment) have essentially identical aspect and vestiture, including spreading hairs (2-storied) on the stem. It seems plausible that all were collected from the same population — none appear to show introgression from *H. pedunculata*.

Chrysopsis villosa var. *minor* Hook., London J. Bot. 6: 244. 1847. *Heterotheca villosa* var. *minor* (Hook.) Semple, Novon 4: 54. 1994. **TYPE**: **Wyoming**. [Natrona Co.]: Protologue: "Oregon Territory, Rocky Mts, granite masses of the Sweet Water River, only fringing the fissures," Jul 1843, *C.A. Geyer 7* (holotype: K; isotypes: GH image!, NY image!).

Semple (1996) noted that the Geyer collection was made in Sweetwater County, but the site where the Sweetwater River crosses granite masses is in southwestern Natrona County, at the Devil's Gate — this narrow gorge was a significant landmark along the Oregon Trail (Plants and Rocks 2014; and see Wikipedia entries for "Devil's Gate (Wyoming)" and "Independence Rock (Wyoming)"). Geyer collected along the Oregon Trail in Wyoming in 1843 with W.D. Stewart's expedition.

Chrysopsis canescens var. *nana* A. Gray, Mem. Amer. Acad. Sci. 4 [Pl. Fendl.]: 78. 1849. *Heterotheca villosa* var. *nana* (A. Gray) Semple, Novon 4: 54. 1994. **TYPE**: **New Mexico**. [Mora Co.]: Protologue: "Elevated rocky region 2 mi E of the Mora River; August. (391c.)," 17 Aug 1847, *A. Fendler 391c* (holotype: GH image!, Fig. 98; isotype: MO!).

Fendler made the collection returning to St. Louis from collecting in the vicinity of Santa Fe, New Mexico, October 1846 through early August 1847. The Santa Fe Trail crossed the Mora River in the vicinity of the present community of Watrous (now along Interstate 25) and Fendler's group was there on 17 August, 1847 (Shaw 1982). The MO isotype gives the name with the number "362," which is the listing number of the species in Gray's published account; "391" is in handwriting at the upper left corner of the label, as is "391c" on the holotype label.

Chrysopsis horrida Rydb., Bull. Torrey Bot. Club 31: 648. 1905. *Heterotheca horrida* (Rydb.) Harms, Wrightia 4:17. 1968. **TYPE**: **Colorado**. [Weld Co.]: New Windsor, 8 Aug 1900, *G.E. Osterhout 2326* (holotype: NY image!; isotypes: RM-3 sheets! images!).

Chrysopsis asprella Greene, Leafl. Bot. Observ. Crit. 1: 150. 1905. **TYPE**: **Colorado.** Montrose Co.: Black Cañon, 7000 ft, 8 Jul 1901, *C.F. Baker 379* (holotype: NDG 53766; isotypes: CORD, DS!, E, GH, MIN, MO!, NY, RM-2 sheets!, RSA-2 sheets, US, VT). Images! of all types except DS. The holotype is a plant of *H. hirsutissima*; some isotypes (e.g., NY) apparently show

introgression from *H. paniculata* or are best identified as *H. paniculata* (see comments under *H. paniculata*).

Chrysopsis compacta Greene, Leafl. Bot. Observ. Crit. 1: 150. 1905. **TYPE**: **Colorado**. [Gunnison Co.]: Jack's Cabin [ca. 5 miles NE of Almont], 8280 ft, 26 Jul 1901, *C.F. Baker 608* (holotype: NDG 53781; isotypes: E, GH, MIN, MO!, NY, RM-2 sheets!, RSA, UC-2 sheets!, US, VT). Images! of all types. The holotype is a plant of *H. hirsutissima*; some isotypes apparently show introgression from *H. paniculata* (see comments under *H. paniculata*).

Chrysopsis arida A. Nels. in Coult. & Nels., Man. Bot. Rocky Mts., 492. 1909. **TYPE**: **Wyoming**. Albany Co.: Tie City, dry sandy hills and cliffs, 20 Jul 1900, *A. Nelson 8224a* (holotype: RM!; isotypes: NEB, NY, VT). Images! of all types.

Heterotheca hirsutissima has a distinct geographic range and usually can be unambiguously identified. The concept here of *H. hirsutissima*, at least in morphology, is essentially the same as that of Harms (1963, 1968), who identified it as *H. horrida*. Plants are characterized by a loosely corymboid capitulescence, lack of capitular bracts, eglandular, (1–)2-storied stem vestiture, the overstory hairs deflexed-spreading and 1–3(–4.5) mm long, and obovate, subpetiolate leaves sessile-glandular on both surfaces. Involucres 8–18 mm wide (pressed), with inner phyllaries 5–9 mm long, eglandular. Ray flowers 12–25.

All chromosome counts for *Heterotheca horrida* /*H. villosa* var. *nana* — except two — are diploid, fide Harms (1963, 1967) and Semple (1996, 2008). A tetraploid count is reported from Taos Co., New Mexico (*Semple & Heard 8055*, see comments below); a triploid is reported from Jefferson Co., Colorado (*Semple 2256*, not seen; Semple 1977). Semple (1996, p. 128) noted that "head size suggests the type [of var. *minor* = *H. horrida* = *H. hirsutissima*] is probably a diploid."

The new combination *Heterotheca hirsutissima* incorporates an earlier name for what has been identified as *Heterotheca horrida* and *H. villosa* var. *nana*, and, in part (including the type), *H. villosa* var. *minor*. Semple placed *Chrysopsis hirsutissima* and *C. arida* as synonyms of *H. villosa* var. *minor*. His concept of var. *nana* is a fairly close match for what is identified here as *H. hirsutissima*; his var. *minor* includes *H. hispida* and many collections of *H. hirsutissima* with upper leaves narrowly to braodly oblanceolate on relatively longer internodes (vs. linear to broadly obong on relatively shorter internodes) and slightly less glandular.

Plants of the type collections of *Heterotheca villosa* var. *minor* (see NY isotype) and *Chrysopsis arida* produce small capitular bracts at low frequency. Plants of *H. hirsutissima* in Baca, Cimarron, and Union counties (Colorado, Oklahoma, New Mexico) produce narrow capitular bracts at a low frequency within populations (ca. 5–10%, pers. observ. in the field) and on individual plants. *Bennett 8787*-BRY (Bernalillo Co.) and *Holmgren 7189*-BRY (Taos Co.) have the habit, leaf morphology, and vestiture of *H. hirsutissima* but have relatively small heads and are atypical of *H. hirsutissima* in producing well-developed, elliptic-oblanceolate capitular bracts (no species in this region of north-central New Mexico consistently produces capitular bracts).

A collection from Valencia Co., New Mexico, has the habit of *Heterotheca hirsutissima* but atypical vestiture — densely glandular with reduced non-glandular vestiture: ca. 5 mi SE of Grants, rest stop on N side of US 40, Malpais lava beds, 24 Jun 1986, *Kass 2465* (BRY).

Semple (1996, p. 142) recognized the similarity between var. *nana* and var. *minor*: "The determination that the type of *Chrysopsis horrida* was more similar to the type of *Diplopappus hispidus* than previously recognized resulted in the recommendation that the two be treated as conspecific and possibly even convarietal (Semple 1990)" but in 1996 he segregated *C. villosa* var. *nana* (including *C. horrida*) and *C. villosa* var. *minor* (including *C. hispida*). "Variety *nana* is distinguished by its linear

to broad oblong, often patent, upper stem leaves and stems with short internodes ... versus narrowly to broadly oblanceolate upper stem leaves in var. *minor* on stems with longer internodes ... Forms of var. *minor* with oblong to ovate leaves generally have stems with longer internodes and fewer leaves" (1996, p. 141; his key on p. 31 separates them essentially in the same way).

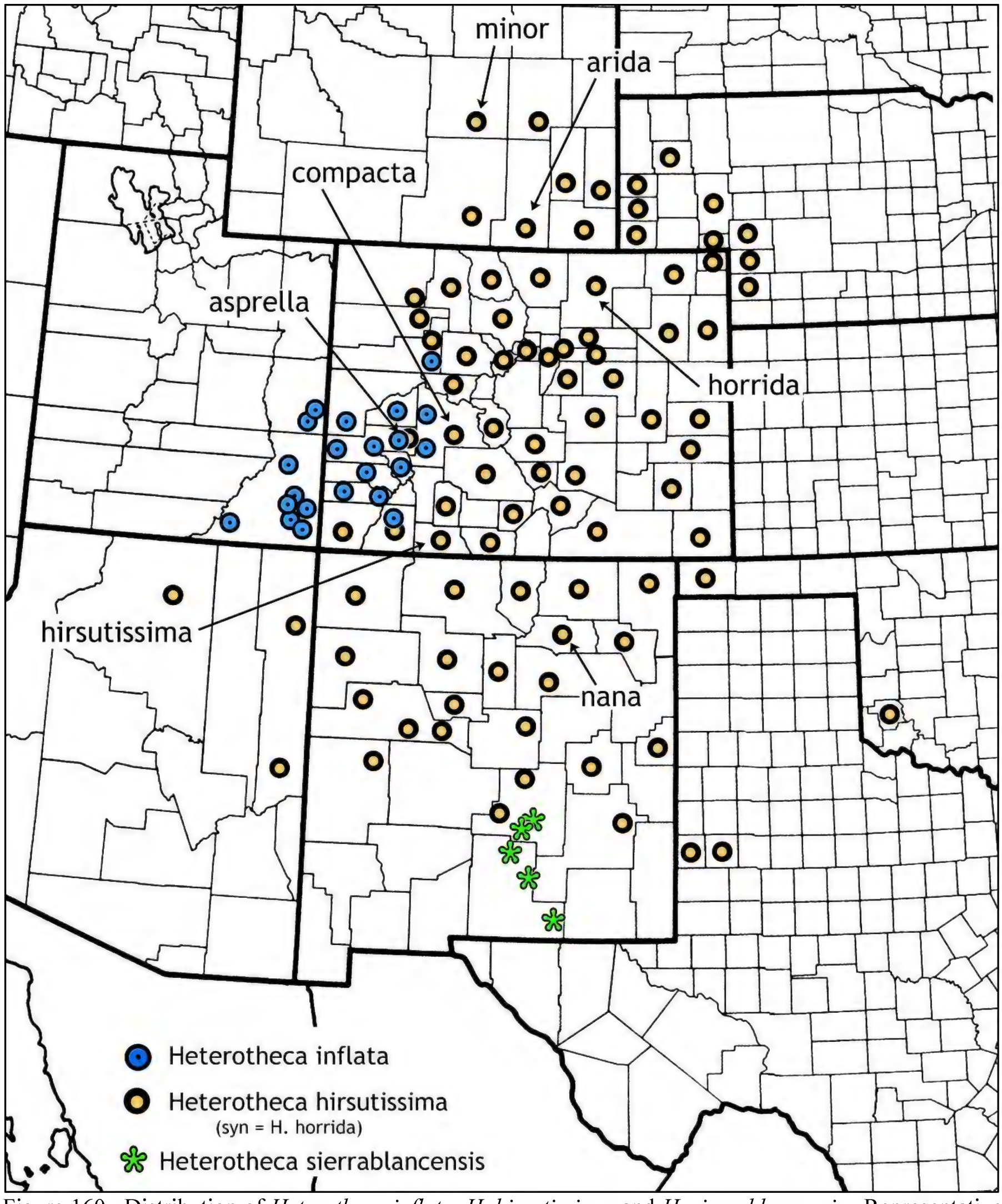


Figure 160. Distribution of *Heterotheca inflata*, *H. hirsutissima*, and *H. sierrablancensis*. Representative outlying collections are cited in the text. Names with arrows are of synonyms of *H. hirsutissima*.

Plants of *Heterotheca hirsutissima* small in stature with small heads and exceptionally small leaves occur in central New Mexico. Gray's *Chrysopsis canescens* var. *nana* is one of these — his varietal epithet ("nana") surely alluded to the small stature (3–4 inches high) of the type and its small leaves and heads ("caulibus 3–4 pollicaribus; foliis capitulisque parvis minus incanis," as in the protologue). The GH type of var. *nana* (like *Cutler 2112* from Valencia Co.) has silvery-sericeous leaves, which is presumably the feature that influenced Gray to place this as a variety of *H. canescens*. Leaves of the MO isotype are strigose-hirsute with shorter hairs but other features are the same.

Collections examined of unusually small-leaved, small-stature plants. **New Mexico**. Lincoln Co.: 2 mi SW of Corona, 15 Jul 1935, *Hubricht et al. B1483* (MO). Torrance Co.: 6.5 km NE of Duran on NMex Hwy 3, rocky broken prairie with scattered juniper, 2 Oct 1995, *Semple 10518* (MO; dups indicated on label as "WAT, BALT, MO, NMC, MONTU"). Valencia Co.: 16 mi N of Trechado, frequent among rocks, 10 June 1938, *Cutler 2112* (CAS, MO).

Exceptionally tall plants of *Heterotheca hirsutissima* occur in north-central New Mexico — these are generally 25–50 cm tall (on herbarium sheets, where probably under-represented in height by collections of small plants) and up to about 100 cm (personal observation, see label comments on *Nesom FW172* from Bernalillo Co.). They appear to be sympatric with plants of typical morphology and may represent a tetraploid race (e.g., see *Semple & Heard 8055*).

Representative collections examined of unusually tall/robust plants. **New Mexico**. Bernalillo Co.: Sandia Mts, Las Huertas Cañon, hillside, 8000 ft, Jul-Aug 1914, *Ellis 211* (MO); Sandia Mts., Allen's Ranch, dry hillsides and among bushes, 7200 ft, 24 Aug 1914, *Ellis 350* (MO); city of Bernalillo, E side of town near Hwy 25, side of large drainage through urban area, plants up to 3 ft tall, with many erect-ascending stems from the base, common, 25 Jul 2002, *Nesom FW172* (BRIT). San Juan Co.: 4 mi SE of Nageezi, 8 mi W of Lybrook Indian Mission, 7000 ft, 20 Jul 1977, *Peabody 1637* (BRY). San Miguel Co.: 2.3 mi SE of Rowe, road cut, red silty clay, 7 Aug 1955, *Shinners 21004* (SMU). Sandoval Co.: 5 mi SE of Cuba, head of El Cajete Canyon, 9000 ft, 10 Aug 1977, *Sears 315* (BRY). Santa Fe Co.: Cerro Negros area, ca. 10 km E of Santa Fe, pinyon pine-scrub, 27 Jul 1983, *Crosby 14689* (MO-2 sheets); Santa Fe Creek valley, rocky hillsides, Jun-Aug 1847, *Fendler 360* (MO); 1/2 mi S of Santa Fe, juniper association, 23 Jul 1961, *Harms 1921* (KANU); 4 mi E of Santa Fe, along Santa Fe Creek, 7500 ft, 3 Jul 1899, *Heller 3807* (MO). Taos Co.: Valley of Rio Pueblo near Picturis Pueblo, 7300 ft, 10 Aug 1966, *Bennett 8785* (BRY); 12.0 km N of Pilar on NM-68, sage, pinyon, juniper scrub, 20 Sep 1985, *Semple & Heard 8055*, **2n=36** (NMC).

Representative outlying collections in Arizona, New Mexico, Oklahoma, Texas, and Utah. **Arizona**. Apache Co.: Canyon de Chelly Natl Mon., dry areas, 5700 ft, 13 Sep 1955, *Demaree 38585* (RSA); Navajo Indian Reservation, P.O. Fort Defiance, rocky dry areas, 7000 ft, 15 Jul 1961, *Demaree 44621* (SMU); Navajo Indian Reservation, P.O. Fort Defiance, dry rocky ridge, open woods, 7000 ft, 15 Jul 1961, *Demaree 44623* (CAS); Petrified Forest Natl Monument, 3 mi N of Puerco Ranger Station, gravel barpits along hwy, 5600 ft, 19 Jun 1941, *Fleming 145* (CAS); Richville Valley, sedimentary badlands, Aug 1938, *Gentry 3825* (RSA). Navajo Co.: 3 mi S of Holbrook, grassland, 5200 ft, 6 May 1981, *Butterwick 7564* (CAS). **Colorado**. Baca Co.: Colorado Road 8 at first creek crossing N of Oklahoma state line, ca. 9-10 mi N of Kenton, abundant on sandstone ledges along S side of creek, with *Ulmus pumila*, 4400 ft, abundant, in early flower, many decumbent-ascending stems from the base, 28 Jul 2015, *Nesom het2015-3* (BRIT, TEX, 3 dups). **New Mexico**. Chavez Co.: Helena Rd [Co. Rd. 11] off Hwy 82, gravelly soil in *Yucca-Gutierrezia-Opuntia* community, 4882 ft, 7 Sep 2002, *Atwood 29008* (BRY). Union Co.: NMex Hwy 551 up Toll Gate Canyon, 1.4 mi N of jct with NMex Hwy 456, ca. 9 mi S of Branson, roadside pullout area, *Juniperus*, *Cercocarpus*, and scattered ponderosa pine on slopes, *Populus* along stream, sandstone area, 6200 ft, abundant along both sides of road, in full flower, 29 Jul 2015, *Nesom het2015-6* (BRIT, TEX, 6 dups). **Oklahoma**. Cimarron Co.: Ca. 2.2 mi E of Kenton on Hwy 325, where hwy passes through large sandstone outcrops, N-facing sites along N side of hwy on small spur road, juniper with scattered oaks and *Cercocarpus*, 4450 ft, abundant in crevices and at base of rock, well into flower, 28 Jul 2015, *Nesom het2015-2* (BRIT, TEX, 9 dups); ca. 5 road mi N of Kenton, rocky canyon, 25 Sep 1976, *Taylor 23751* (LSU image!). Greer Co.: N edge of Granite, from a granite rock, 9 Jul 1976, *Taylor 22526* (BRIT). **Texas**. Terry

Co.: Fitzgerald Ranch Preserve, ca. 1.2-1.3 mi E of FM 1780 along internal road from gate 5.1 road mi N of jct with FM 2196, occasional in sandsage-Havard oak-dropseed vegetation, on and around low dunes, 3570 ft, 10 Sep 2008, *Carr 27128* (TEX); Wellman, sandy soil dominated by slum oak, 8 Jul 1934, *Reed 3787* (TEX). Yoakum Co.: Ca. 0.2-0.3 mi E of FM 1780 from a point 5.1 road mi N of its jct with FM 2196, occasional in sandsage-Havard oak-dropseed vegetation on low hummocky topography on essentially level part of Holocene sand sheet, 3585 ft, 9 Sep 2008, *Carr 27080* (TEX, Fig. 168).

The long-disjunct collection from Greer Co., Oklahoma, is confidently identified as *Heterotheca hirsutissima*. In Texas, the Yoakum Co. collection of *H. hirsutissima* is typical in morphology; in Terry Co., the vestiture of both collections suggests an influence from *H. angustifolia*; a collection of *H. angustifolia* from Terry Co. (10 Jul 1941, *Tharp 42-83*, LL) is typical except for elongate peduncles, which suggests reciprocal gene flow with *H. hirsutissima*. Similar introgression appears to occur in southwestern Colorado (e.g., Las Animas Co.).

Apparent distantly disjunct collection. MEXICO. **Nuevo León**. Ca. 1.5 mi below the microwave station on Cerro Potosí, N of Galeana, in douglas fir and oak forest, Sep 1970, *Norris 17744* (CAS) — 3 plants on the sheet. This collection is far out of range but provisionally identified here as *Heterotheca hirsutissima*, although the densely leafy stems, very short peduncles (2–10 mm long), and thin-based hairs are not characteristic of that species. Semple annotated the specimen in 1987 as *H. horrida*; he cited it in 1996 as H. "aff. harmsiana." There is no Mexican species to which the Norris collection is closely similar, nor any (besides *H. hirsutissima*) in Texas or New Mexico. It seems unusual that only a single collection has been made, since numerous botanists have collected on Cerro Potosí, but the three plants on the Norris sheet are consistent in morphology and apparently were representative of a population. No species of *Heterotheca* has been reported from the summit area of Cerro Potosí (Beaman & Andresen 1966; Garcia & González 1991).

Figure 161. *Heterotheca hirsutissima*, holotype NDG.

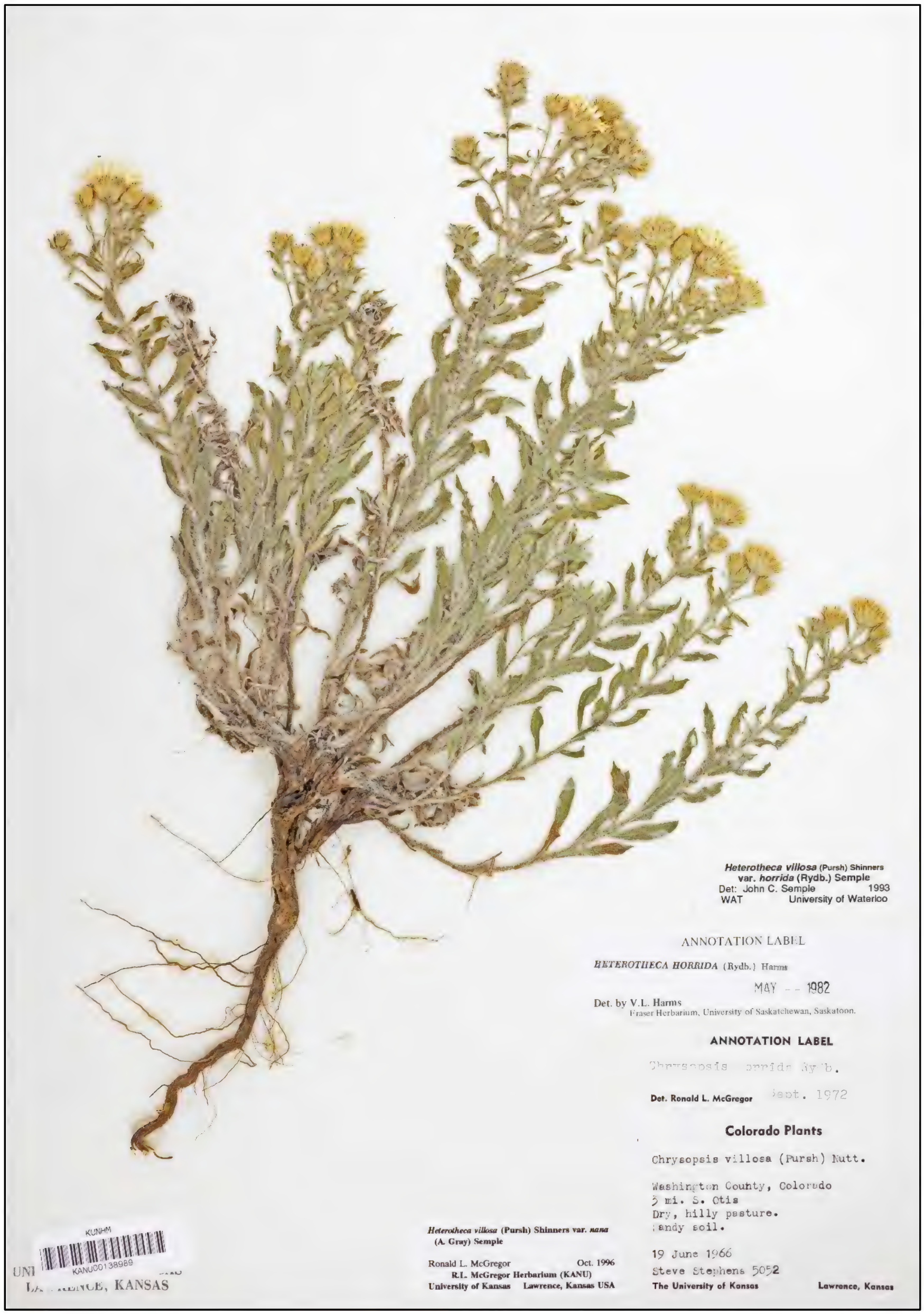


Figure 162. *Heterotheca hirsutissima*. Washington Co., Colorado. *Stephens 5052* (KANU).

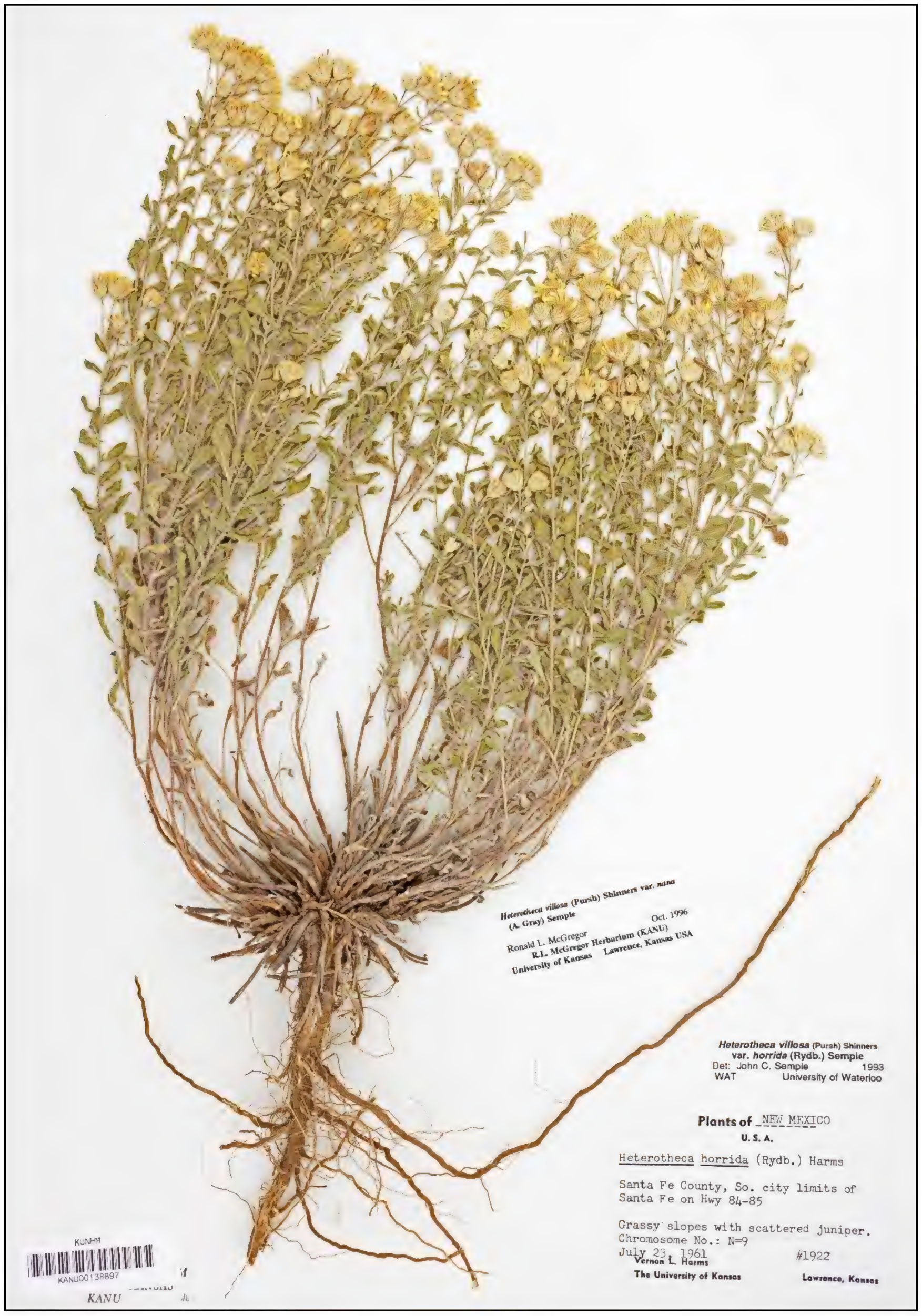


Figure 163. *Heterotheca hirsutissima*. Santa Fe Co., New Mexico. *Harms 1922* (KANU). Typical morphology; diploid by chromosome count.

Figure 164. *Heterotheca hirsutissima*. Santa Fe Co., New Mexico. *Harms 1921* (KANU). Robust plant with unusual morphology ("large offsets from root"), perhaps tetraploid (see text).

Figure 165. *Heterotheca hirsutissima*. Bernalillo Co., New Mexico. *Holmgren 7404* (KANU).

Figure 166. *Heterotheca hirsutissima*. Colfax Co., New Mexico. *Legler 10398* (UNM).

Figure 167. *Heterotheca hirsutissima*, probably Mora Co., New Mexico. Holotype of *Chrysopsis canescens* var. *nana* (GH).

Figure 168. *Heterotheca hirsutissima*, Yoakum Co., Texas. *Carr 27080* (TEX).

31. HETEROTHECA SIERRABLANCENSIS (Semple) Nesom, Sida 22: 374. 2006. *Heterotheca villosa* var. *sierrablancensis* Semple, Univ. Waterloo Biol. Ser. 37:146. 1996. **TYPE**: **New Mexico**. Lincoln Co.: Sierra Blanca, NM Hwy 532, road to Ski Resort, 8.5 km W of NM Hwy 48, rocky outcrop and face of roadcut at switchback directly below scenic overlook, 2 Oct 1995, *J.C. Semple 10513-A*, 2*n*=18 (holotype: WAT; isotypes: MO!, UC!). Semple (1996) cited the isotype distribution also to NMC, RM, and WAT.

Heterotheca sierrablancensis apparently is closely related to *H. hirsutissima,* perhaps directly derived from it or sharing an immediate common ancestor. Both species have spreading stem vestiture and characteristically lack capitular bracts. *Heterotheca sierrablancensis* is distinct in its larger, mostly oblanceolate-oblong to lanceolate-oblong cauline leaves densely strigose and with densely glandular leaf surfaces, its relatively long ray flowers (10–14 mm) with broad (1.5–3 mm) ligules, and closely and finely strigose phyllaries. Stems are mostly 20–35(–46) cm (including field observations by Semple) and erect from the base, usually single- or few-stemmed (compared to the caespitose habit of *H. hirsutissima*). It is endemic to Lincoln and Otero counties, mostly in the White Mountains and most abundantly in the Sierra Blanca area, at 7200–11,500 feet elevation. The few collections of typical *H. hirsutissima* that have been made in Lincoln County appear to be morphologically and ecologically distinct from *H. sierrablancensis*. Chromosome number, 2*n*=18 (*Harms 1801-1*, *Semple 10513-A*, *10513-B*, Lincoln Co.).

Additional collections examined: **New Mexico**. Lincoln Co.: Capitan Mts, Lincoln Natl Forest, 3 mi E of Capitan Pass, 10 mi NE of Capitan, 2500-2700 m, 26 Jul 1964, *Baad 893* (WTU); Sierra Blanca, at N border of Mescalero Indian Reservation, 10 mi NW of Ruidoso, E-facing slope, 24 Jul 1964, *Baad 948* (WTU); 3 km NNW of central Ruidoso, Cedar Canyon 1.9 km SE of its confluence with Musket Ball Canyon, secondary *Pinus ponderosa* forest, 6950 ft, 16 Aug 2015, *Baker 18428* (ASC); Capitan Mts, Seven Cabins Spring (Rd 256) to W Lucero Canyon (Rd 616), 23 Aug 1992, *Dale & Sanderson s.n.* (BRIT); Gray's Peak, 6500 ft, 25 Jul 1900, *Earle & Earle 167* (MO-2 sheets, NMC, POM); Lincoln Natl Forest, White Mts Trail, 8200 ft, 1925, *Ewing E-93* (RM); White Mts, 1.7 mi N of Ruidosa, abundant in roadside clearing in ponderosa pine woods, 7 Jul 1961, *Harms 1801-1*, **n=9** (KANU); White Mts, Skyline Picnic area, 1 mi S of Monjeau Lookout, gravel loam, ca. 9000 ft, 2 Jul 1969, *Hutchins 2220* (UNM image!); White Mts, vicinity of Bonita Lake, gravel loam, ca. 7400 ft, 5 Sep 1971, *Hutchins 3655* (UNM image!); E slopes of Sierra Blanca on road toward ski area (Hwy 532), 11 mi W of Alto, area of spruce and douglas fir, 10,600 ft, 23 Jul 2002, *Nesom FW167* (BRIT); Sierra Blanca, western slope, 18-20 Oct 1922, *Pilsbry s.n.* (PH); Sierra Blanca, NMex Hwy 532, roadway to Ski Resort, 8.5 m from NMex Hwy 48, rocky face and roadcut directly below overlook, 2 Oct 1995, *Semple 10513-B*, **2n=18** (NY); Sierra Blanca, W of Alto on NMex Hwy 532, E of Windy Point Vista, igneous roadcut and exposed rocky slope, 21 Sep 1985, *Semple & Heard 8116* (BRIT, NY); Capitan Mts, R15E, T85, Sec. 16, ponderosa pine-gambel oak, 2160 m, 2 Oct 1982, *Sivinski s.n.* (UNM image!); White Mts, Eagle Creek Canyon, ca 6 air mi NW of Ruidoso, where the creek bends to the SE, granitic outcrop 200 ft above the creek, mixed conifer-oak forest, 8200 ft, crevices in cliff faces, 17 Jun 1981, *Soreng & Ward 1608* (NMC); Sierra Blanca, Lincoln Natl Forest, open slope above Windy Vista Point, grassy slope with scattered *Pinus flexilis*, ca. 3000 m, 28 Aug 1976, *Wagner & Sabo 2506* (UNM); White Mts, 6800 ft, 31 Jul 1897, *Wooton 263* (MO, NMC, NY-2 sheets, POM, RM, UC); White Mts, 6200 ft, 20 Aug 1897, *Wooton 366* (MO-2 sheets, NY); White Mts, White Mtn Peak, 1 Aug 1901, *Wooton s.n.* (NMC); White Mts, 7400 ft, 25 Aug 1907, *Wooton & Standley 3419* (DS, IND, NMC, RM); White Mts, SE slope of Nogal Peak along hiking trail 25, grassy open area on rock outcrop, 9000 ft, 22 Aug 1979, *Worthington 5065* (COLO, UTEP). Otero Co.: Sacramento Mts, James Canyon, 31 Aug 1952, *Dittmer 8073* (UNM image!); Guadalupe Mts, W side of Guadalupe's, 3 mi W of Lincoln Natl Forest, 5800 ft, 10 Aug 1977, *Fletcher 2472* (UNM image!); 15S, 14E, Sec 4, aspen hillside, 17 Aug 1938, *Humphrey 36* (UNM); 9 mi W of Ruidoso on Hwy 70, gravel loam of roadside, 7200 ft, 5 Sep 1971, *Hutchins 3691* (UNM); Apache Indian Reservation SW of Ruidoso, 3.7 mi along US 70 NE of jct with NM Rte 24, ponderosa pine with scattered Douglas fir, white pine, and Gambel's oak, roadside, ca. 7400 ft, 7 Sep 1988, *Keil 14159* (OBI); 6 mi NE of Mescalero, weed patch near Rte 70, 14 Sep 1960, *Martin 4505* (UNM); Monjeau Peak, 500 ft below Monjeau Lookout, 4 mi N and 5 mi W of Ruidoso, 10,000 ft, 14 Sep 1960, *Martin 4514* (UNM

image!); SW of Ruidoso on US Hwy 70 at jct of NMex Hwy 24, road embankment, 22 Sep 1985, *Semple & Heard 8155* (UC); NM Hwy 24, 1/2 mi S of jct Hwy 130, toward Weed, 8 Sep 1979, *Soreng & Spellenberg 594* (NY); along Tularosa Creek, 30 Jul 1897, *Wooton s.n.* (NY); Tularosa Creek, 18 Aug 1899, *Wooton s.n.* (NMC).

Hutchins 3655 from Bonita Lake in Lincoln County is atypical of *Heterotheca sierrablancensis* — it has sessile-petiolate leaves and heads loosely paniculate with small capitular bracts, perhaps reflecting genetic influence of *H. cryptocephala* or *H. fulcrata*. Heads are large with relatively broad rays and stem vestiture is spreading. *Keil 14159* from Otero County has narrow capitular bracts but otherwise matches H. *sierrablancensis*.

Figure 169. *Heterotheca sierrablancensis*. Lincoln Co., New Mexico. *Wagner & Sabo 2506* (UNM).

Figure 170. *Heterotheca sierrablancensis*. Lincoln Co., New Mexico. *Baker 18428* (ASC).

Figure 171. *Heterotheca sierrablancensis*. Monjeau Lookout area, Otero Co., New Mexico. *Hutchins 2220* (UNM).

Figure 172. *Heterotheca sierrablancensis*. Monjeau Lookout area, Otero Co., New Mexico. *Findley s.n.* (UNM).

Figure 173. *Heterotheca sierrablancensis*. Monjeau Lookout area, Otero Co., New Mexico. *Martin 4514* (UNM).

32. HETEROTHECA RUTTERI (Rothr.) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis villosa* var. *rutteri* Rothr., Rep. U.S. Geogr. Surv., Wheeler, Vol. 6, Botany 6: 142. 1879. *Chrysopsis rutteri* (Rothr.) Greene, Erythea 2: 96. 1894. **TYPE**: **Arizona.** [Cochise Co.]: Protologue: "Sanoita Valley, Arizona (662)," *C. Wright 662*(?) (holotype: GH image!). Annotation by W.T. Kittredge in 2008, following Wright's field notes: "Field #513, 2nd coll., '14 Sept., valleys of Sonora, few branches from root' between San Pedro and Sonoita Rivers, Cochise Co., Arizona."

Heterotheca rutteri is characterized by its relatively dense, silvery-sericeous to light green vestiture and few, large heads nearly completely obscured by large, lanceolate-ovate capitular bracts. Ray flowers 15–35. Plants rarely are more greenish with reduced vestiture (e.g., *Reeves R1037* from the Santa Rita Mts). The species is known only from Pima Co., Santa Cruz Co. and Cochise Co. (Huachuca Mts) and localities in closely adjacent Sonora (representative collections cited below). Semple (1996, p. 81) noted that "It is one of those species that once seen is never confused with another taxon."

MEXICO. **Sonora**. 6 mi S of Nogales, open field along RR tracks, ca. 4000 ft, *Matthews 481* (COLO image!); N of Cananea, Los Fresnos cienega, *Warren et al. s.n.* (ARIZ, as cited by Semple 1996).

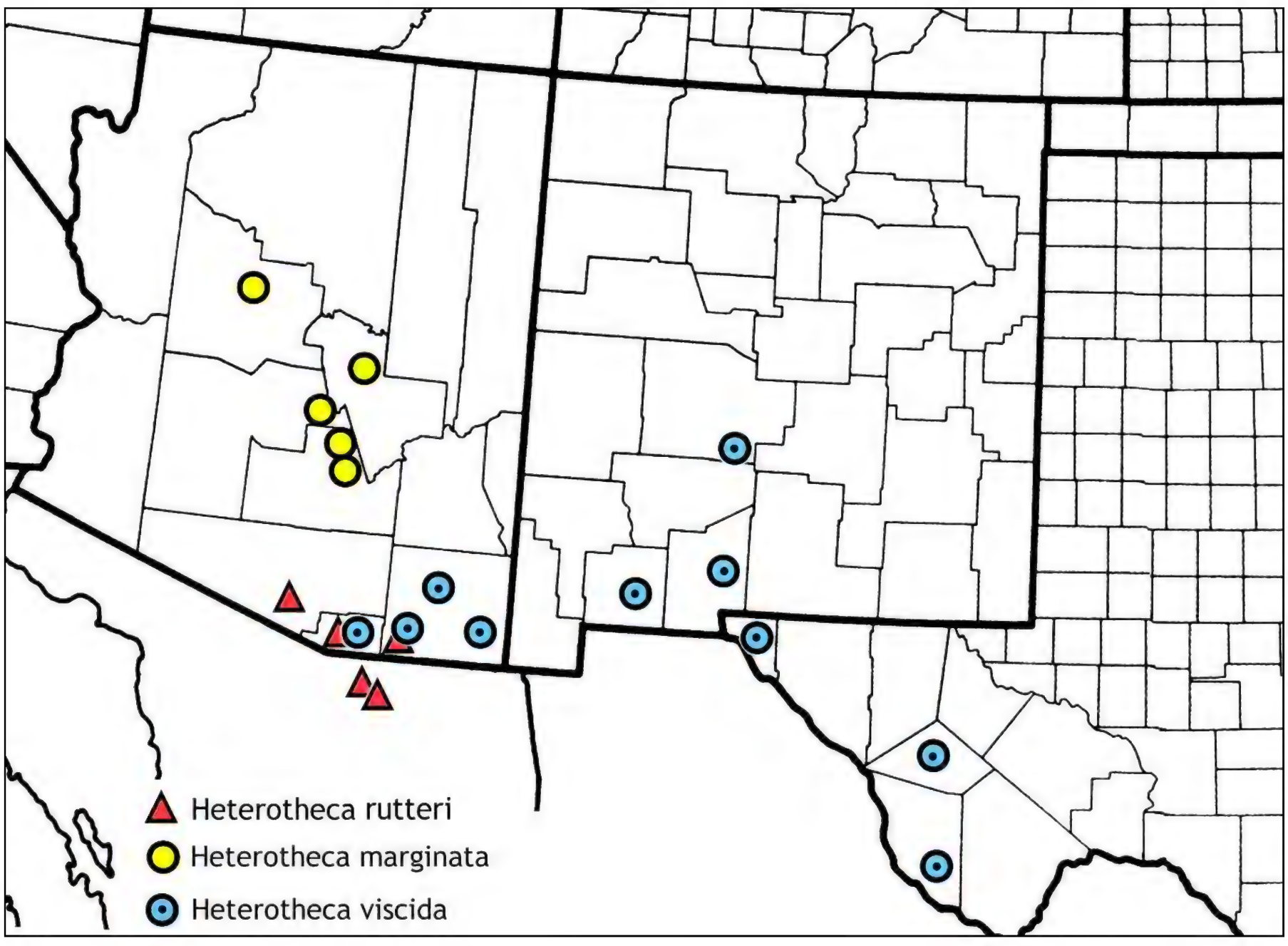


Figure 174. Distribution of *Heterotheca rutteri*, *H. marginata*, and *H. viscida*.

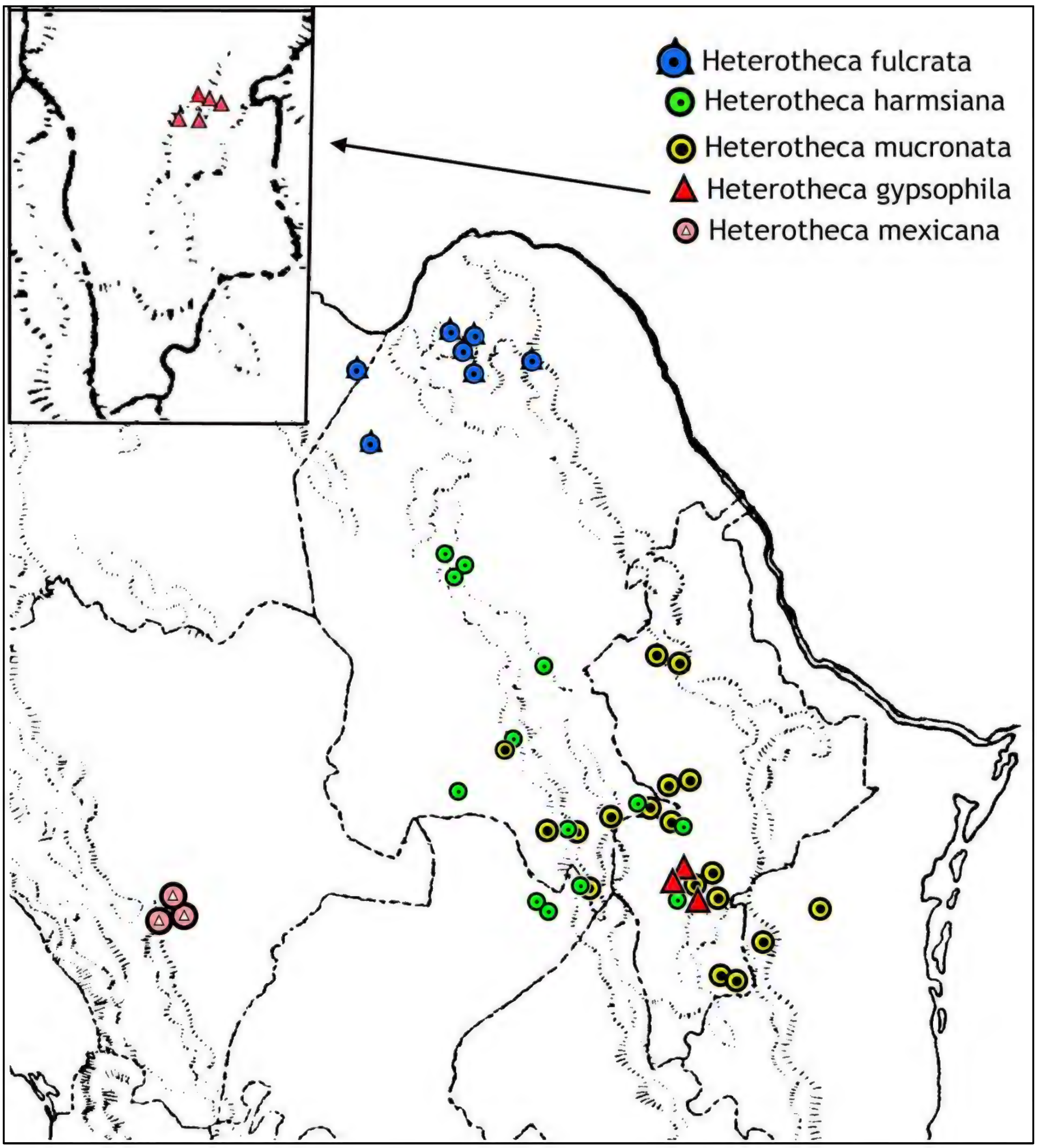


Figure 175. Distribution of Mexican species of sect. *Chrysanthe*. Distribution of *H. fulcrata* in the USA is shown in Fig. 235.

33. HETEROTHECA MUCRONATA Harms ex Turner, Phytologia 55: 205. 1984. **TYPE**: **MEXICO**. **Nuevo León**. Puerto de Santa Ana, ca 15 mi SW of Galeana, common on an unwooded slope, 28 Jun 1934, *C.H. Mueller 934* (holotype: TEX!; isotype: A image!).

Plants of *Heterotheca mucronata* are characterized by their colonial habit from rhizomes or slender, fibrous-rooted caudex branches, producing decumbent-ascending, often unbranched (or 1–2-branched) stems. Stems are loosely strigose to villous, with antrorse or retrorse hairs. Leaves obovate to elliptic-obovate or spatulate-obvate, 4–15 mm wide, entire or with 1–3 pairs of shallow teeth, surfaces loosely strigose to strigose-sericeous, usually sessile-glandular surfaces. Plants from Tamaulipas and from near Linares, Nuevo León, tend to have eglandular leaves and a more densely sericeous vestiture of thinner-based trichomes (more like *H. gypsophila*) than those elsewhere. Heads on ebracteate or minutely bracteate peduncles 1–5 cm long; involucres 8–16 mm wide, 8–11 mm high; ray flowers 12–30, ligules often drying with an abaxial purple midstripe.

Rocky or gravelly habitats, usually in limestone, oak and pine-oak woodlands; 6000-11,600 ft. Chromosome numbers $2n$=18, 36.

A collection from the Sierra de la Paila, where typical *Heterotheca harmsiana* is known to occur, has long peduncles and densely strigose leaves more like *H. mucronata*, but the upper branching is more like *H. harmsiana*. Root and caudex were not collected. **Coahuila**. Mpio. Ramos Arizpe: Sierra de la Paila, Ejido El Cedra, camino hacia el valle de parreños, oak-pine-juniper, 1800-1900 m, 4 Oct 1989, *Villarreal 5341* (BRIT, MO, TEX-2 sheets).

34. HETEROTHECA GYPSOPHILA B.L. Turner, Phytologia 55: 206. 1984. **TYPE**: **MEXICO**. **Nuevo León**. [Mpio. Galeana], 4 mi N of Pablillo, on bank of gypsum arroyo in pinyon forest, 21 Jul 1958, *D.S. Correll & M.C. Johnston 19919* (holotype: LL image!; isotypes: NY image!, TEX-2 sheets!).

Heterotheca gypsophila has been collected only in a small area of exposed gypsum south of Galeana (vicinity of Pablillo), Nuevo León, in oak-pine to pine woodlands at 1250–2050 meters, and within the geographic range of *H. mucronata*. Chromosome number, $2n$=36. It is similar to *H. mucronata* in most features, including its rhizomatous habit, solitary heads, and oblong-spatulate leaves but different in its densely sericeous, white to silvery vestiture of stiff, closely appressed hairs completely obscuring the surfaces. The stems also are sericeous but produce a few stiffly spreading hairs. Leaves are eglandular and proximal margins commonly have long, stiffly spreading cilia. The distinction between *H. gypsophila* and *H. mucronata*, apparent mostly in vestiture, suggests that a reciprocal transplant study might indicate whether differences are more phenotypic than genetic, but its discrete geographic range and its absence in other gypsum areas near Galeana suggest that *H. gypsophila* is a real entity.

35. HETEROTHECA HARMSIANA (Semple) Nesom, **comb. et stat. nov.** *Heterotheca mucronata* var. *harmsiana* Semple, Univ. Waterloo Biol. Ser. 37 (Rev. Heterotheca Phyllotheca), 60. 1996. **TYPE**: **MEXICO**. **Zacatecas**. Road above Concepción del Oro, ca. 8 mi W of jct Rte 54, rocky cactus hillsides, ca 8300 ft, 18 Jun 1976, *D.J. Pinkava et al. P13486* (holotype: ASU as cited in the protologue, not located; isotype: WAT not seen).

Plants caespitose from a woody taproot. Stems erect to ascending-erect, 15–40 cm high, sparsely to moderately and evenly hirsute with slightly deflexed hairs, minutely glandular. Cauline leaves evenly distributed, narrowly oblanceolate to oblanceolate-spatulate, mostly (15–)25–40 mm long and 3–8 mm wide, basally attenuate, often to a narrow petiolar region, surfaces sparsely and loosely strigose to hirsute-villous, eglandular or minutely and inconspicuously sessile-glandular, cilia of leaf and bract margins relatively thin-based (vs. pustulate-based). Heads solitary on sparsely leafy or bracteate peduncles 5–35(–50) mm long, often with subfoliaceous bracts near the heads; involucres

9–15 mm wide, 8–10 mm high, phyllaries eglandular or glandular only at the very apex, otherwise glabrous to sparsely strigose with fine, closely appressed hairs. Ray flowers 12–18. Chromosome number, 2*n*=18 (made by Semple from the type collection of *H. mucronata* var. *harmsiana*).

Flowering Jul–Sep(–Oct). Pine, pine-agave, oak-pine, oak chaparral, chaparral (including agave-cactus); 5000–9200 (–10,000) ft.

Diagnostic features of *Heterotheca harmsiana* are its woody taproot and caespitose growth habit, narrowly oblanceolate to oblanceolate-spatulate leaves with an attenuate, subpetiolate base, and spreading-deflexed stem vestiture. *Heterotheca mucronata* var. *harmsiana* was said by Semple to differ from typical *H. mucronata* by "fewer hairs and more glands" and he mapped both taxa using vestiture as a criterion, identifying them at the same localities in some areas of Nuevo León and Coahuila. Plants of *H. harmsiana*, however, are caespitose and arise from a woody taproot (vs. colonial from rhizomes in *H. mucronata*), stems are erect and have a tendency to be unbranched (vs. decument-ascending and branching distally), leaves are narrowly oblanceolate (vs. broadly obovate to elliptic-obovate in *H. mucronata*). The two are sympatric in central Nuevo León and where their ranges are contiguous or overlapping in southeastern Coahuila (in the Sierra de la Viga and Sierra Zapalinamé) and along the Coahuila-Zacatecas border (Sierra Astillero, e.g., H. harmsiana: *Henrickson 6284*; H. mucronata: *Henrickson 13302c Johnston, Wendt, & Chiang 11571*). Both species occur in the Sierra de la Paila, northwest of Saltillo.

Additional collections examined. MEXICO. Coahuila. Sierra de Parras, ca. 10 km W of Parras de la Fuente, 4 Nov 1972, *Chiang et al. 10070B* (LL); ca. 35 air mi W of Cuatro Cienegas, mid Canyon de la Hacienda of Sierra de la Madera, oak-pine forest, alluvial limestone stream bed, 6000 ft, 6 Aug 1973, *Henrickson 12005* (ASU, MEXU image, RSA, TEX); ca. 22 air mi WNW of Cuatro Cienegas, upper portion of limestone Canyon de la Hacienda, below 1st lumber camp in Sierra de la Madera, oak-pine forest, 5000-6000 ft, 28 Sep 1973, *Henrickson 13633* (ASU, MEXU image, MO, NY, RSA, SRSC image); 29 air mi WNW of Cuatro Cienegas, N slope of the Sierra de la Madera, ca. 7.5 air mi W of Rancho Cerro de la Madera, with lower chaparral-oak scrub at base of Cañon Desiderio, in upper Cañon Posos, 1700-1800 m, 13 Aug 1976, *Henrickson 15341* (MEXU image, NMC, NY, RSA, TEX); Cuatro Cienegas Basin, Sierra Madera, 1968, *Minckley s.n.* (ASU digital image!); Monclova, Gloria Mts, Jul 1939, *Marsh 1892* (TEX); Canon de San Lorenzo, 5 km SW de Saltillo, carr. Saltillo-Concepción del Oro, 1900 m, 5 Jun 1989, *Martinez 1861* (TEX); Sierra Guadalupe, S of La Cuchilla, ledges of limestone rocks, 2400-2500 m, 15 Jul 1934, *Pennell 17380* (PH); Cerro de la Viga, ca. 4 mi E of Jame, logging road, pines, 10,000 ft, 15 May 1981, *Poole 2274* (MEXU image, TEX-2 sheets); S of Saltillo, mountain sides, K884, 29 Jul 1929, *Runyon 1324* (TEX); Mpio. Ramos Arizpe, Sierra de la Paila, Ejido el Cedral por el canon El Carmen, bosque esparcido de *Quercus glaucoides*, *Q. gravesii*, *Pinus arizonica*, y *Juniperus flaccida*, suelo calcareo, 1300-1600 m, 26 Aug 1992, *Valdés et al 2221* (MEXU image); Las Vigas, Sierra Arteaga, Canon de la Carbonera, 2100-2600 m, [1991], *Villarreal & Carranza 3791* (TEX). **Nuevo León**. Mpio. Galeana, El Carrizo, trailside, pine woods, 1740 m, 27 Jun 1983, *Hinton 18471* (GBH - mixed collection, with *H. gypsophila*); Mpio. Montemorelos, El Butano, bosque coniferas-encino, 2000 m, 3 Jul 2004, *Estrada et al. 16317* (BRIT). **Zacatecas**. 3.1 road mi above Concepción del Oro, ridge W of city, S-facing granite slopes, agave-cactus, 8000 ft, 30 Aug 1971, *Henrickson 6284* (ARIZ, MEXU image, NY, RSA, TEX); ca. 15 air mi E of Concepción del Oro, 2.5 mi NE of Guadalupe Garceron in small ravine NW of summit of igneous Sierra del Astillero, 6500 ft, 22 Sep 1973, *Henrickson 13302c* (ARIZ, RSA, TEX); 1 km E of Aranzazu and 6 km W of Concepción del Oro, 29 Mar 1973, *Johnston, Wendt, & Chiang 10476* (TEX); Sierra del Astillero (approached from SE, from Tanque El Alto), extensive chaparral and oaks, lower slope with *Yucca carnerosana*, *Dasylirion*, upper slope with *Pinus ponderosa*, *Agave macroculmis*, 2 Jul 1973, *Johnston, Wendt, & Chiang 11571* (MEXU digital image).

Figure 176. *Heterotheca mucronata*, showing colonial habit. Mpio. Arteaga, Coahuila. Photo by David Mercado-Morales, Naturalista.

Figure 177. *Heterotheca mucronata*. Mpio. San Pedro Garza García, Nuevo León. Photo by E. Tadeo Hernández A., Naturalista.

Figure 178. *Heterotheca mucronata*. Santiago, Nuevo Leon. Photo by Carlos G. Velazco-Macias, Naturalista.

Figure 179. Representative plants of *Heterotheca mucronata*, from Nuevo León and Tamaulipas.

Figure 180. Representative plants of *Heterotheca harmsiana*, all from Coahuila.

36. HETEROTHECA MEXICANA Harms ex Turner, Phytologia 55: 204. 1984. **TYPE: MEXICO. Durango**. Fields along Rte 40, ca 31 mi SW of Durango, 16 Aug 1960, *R.M. King 3748* (holotype: TEX! image!).

Heterotheca mexicana is endemic to the area around the city of Durango, where it grows at 1900–2600 meters in rocky meadows, grassslands, roadsides, and openings in oak or pine forests. It is similar to *H. mucronata* in habit, vestiture, leaf morphology, tendency for solitary heads on merely bracteate peduncles but is distinctive in its thick woody taproot, longer peduncles, and weakly developed outer pappus of lanceolate scales or bristles. Chromosome number, $2n$=18. Not sympatric with any other species.

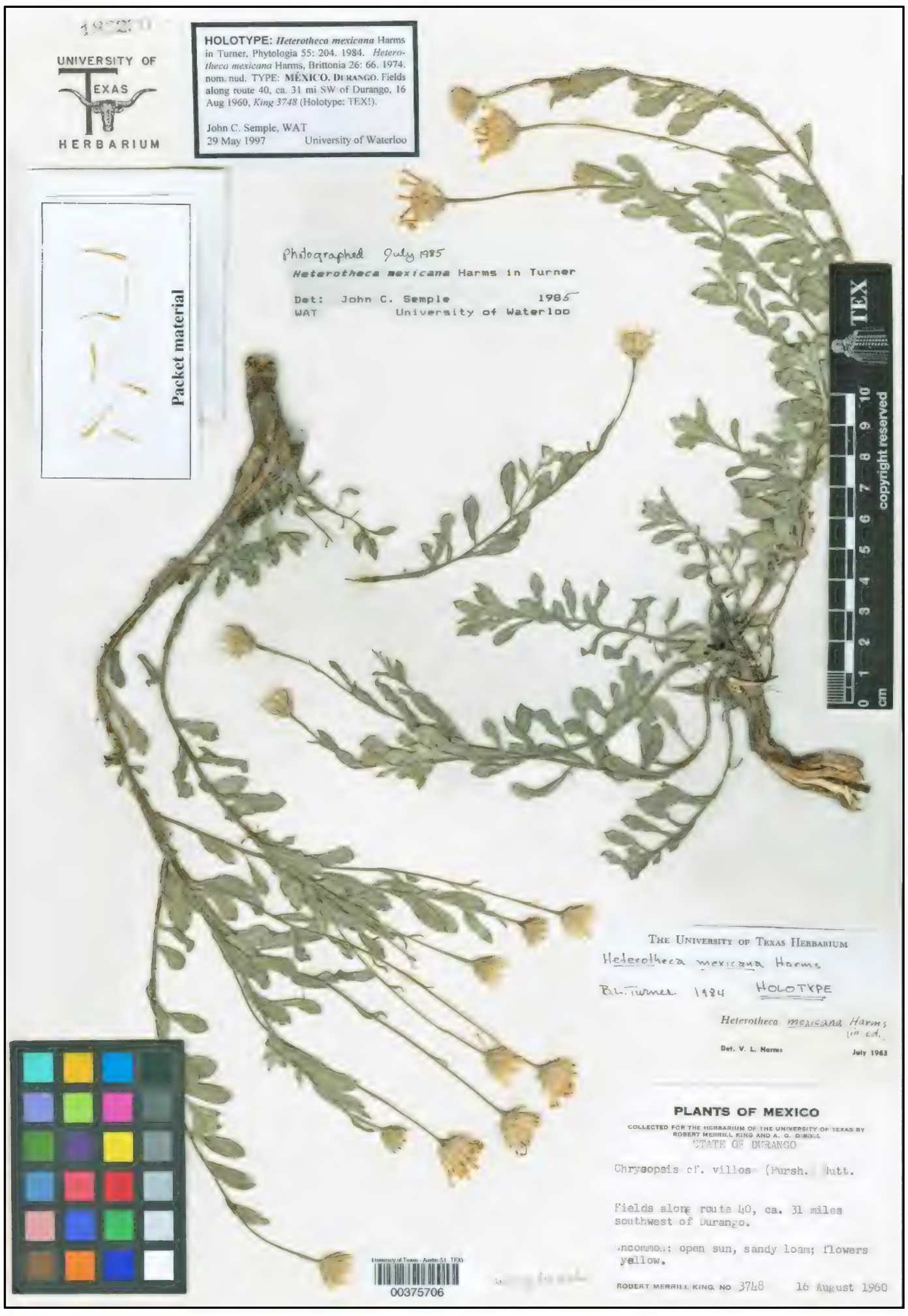


Figure 181. *Heterotheca mexicana*. Holotype (TEX).

37. HETEROTHECA VISCIDA (A. Gray) Harms, Rhodora 70: 302. 1968. *Chrysopsis villosa* (Pursh) Nutt. var. *viscida* A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. *Chrysopsis viscida* (A. Gray) Greene, Erythea 2: 96. 1894. **LECTOTYPE** (Harms 1968): **Arizona**. Santa Cruz Co.: Santa Rita Mts., clefts of dry ledges, 7500 ft, 28 May 1881, *C.G. Pringle s.n.* (GH!; isolectotypes: NY-3 sheets images!, PH!).

Heterotheca viscida usually is unambiguously identified, characterized by its decumbent to decumbent-ascending habit, sessile-glandular to glandular-viscid (stems, leaves, involucre) and sparsely hirsute (or nearly glabrate except for marginal cilia and hairs along veins) vestiture. Leaves broadly elliptic-oblanceolate to obovate or obovate-spatulate, dark green (partly because of low density of non-glandular hairs), proximal with subpetiolate bases but distal often becoming sessile and subclasping. Heads mostly solitary (a second head occasionally produced on a short branch), without capitular bracts. Chromosome number, $2n$=18.

Semple (1996) observed that *Heterotheca visicida* in Texas sometimes has oblanceolate leaves and smaller heads and may resemble *H. arizonica* and *H. fulcrata* in these aspects — both of the latter, however, consistently have prominent capitular bracts. The apparently disjunct populations of *H. viscida* in Texas (Jeff Davis and Presidio counties) are in the morphological range of those further west.

Representative collections examined. **Arizona**. Cochise Co.: **Chiricahua Mts**: Rustler's Park, rock crevices, 9000 ft, 18-19 Jun 1930, *Goodman & Hitchcock 1187* (UC); Chiricahua Wilderness Area, Rucker Canyon, 7650-7700 ft, 17 Sep 1976, *Leithliter 753* (ASU); Chiricahua Natl Monument, Sugarloaf Mt near trail to lookout tower, crevice of rhyolite tuff, Quercus and shrubs, 7100 ft, 10 Aug 1974, *Reeves R982* (ASU); Ida's Peak along Telephone Trail from "Locust Camp," Pinery Canyon, 8000 ft, 5 Jul 1919, *Stone 301* (PH). **Dos Cabezas Mts**: Around "heads," 8000 ft, 13 Jul 1977, *Bingham 2658* (ASU). **Dragoon Mts**: Stronghold Canyon East, 5600 ft, 2nd major waterfall/bedrock area in major drainage, 23 Oct 1992 (ASU, DES). **Huachuca Mts**: Black Bear Mine, along trail in Lutz Canyon, cliff face with *Cercocarpus*, *Arbutus*, *Agave parryi*, ca. 7800 ft, 9 May 1992, *Bowers 3645* (ASU); top of Montezuma Peak, oak and pinyon, 7000-7600 ft, 16 Jul 1990, *Parfitt 4392* (ARIZ); dry cliffs, 3 Jul 1884, *Pringle s.n.* (PH). Santa Cruz Co.: **Santa Rita Mts**: trail to Mt Wrightson, 2700 m, 4 Jul 1991, *Fishbein s.n.* (ARIZ); trail from Madera Canyon to Mt Wrightson, 9400 ft, 12 Aug 1945, *Parker 5855* (UC); clefts of dry ledges,700 ft, 28 May 1881, *Pringle s.n.* (PH-2). **New Mexico**. Doña Ana Co.: **Organ Mts**: On and in vicinity of Organ Needle, E side of Organ Needle, among rocks, 8850 ft, 20 Oct 1979, *Spellenberg & Dunford 5432* (NMC). Luna Co.: **Florida Mts**: N side of Baldy Peak, limestone ledge just below top, 6600 ft, 1 Sep 1997, *Worthington 27037* (UNM); 1.6 air mi WNW of top of Gym Peak, 5800 ft, 12 Jul 1991, *Worthington 19594* (UTEP). Socorro Co.: **Mockingbird Mts.**: White Sands Missile Range, ca. 55 air mi E of San Antonio, between San Andres and Oscura Mts, just S of major saddle, NNE granitic cliffs, shaded, especially in clefts, with *Quercus gambelii*, *Fraxinus velutina*, *Solidago wrightii*, in tufts from cracks in deep shade, 2090 m, 3 Sep 1990, *Spellenberg et al. 10597* (ID, NMC). **Texas**. El Paso Co.: **Franklin Mts**: Canutillo, rocky ravines, 12 Jul 1911, *Barlow s.n.* (UC); 0.5 air mi NE from the top of North Franklin Mtn, ca. 6400 ft, 27 Aug 1988, *Worthington 17084* (OBI). Jeff Davis Co.: **Davis Mts**: ca. 0.7 air mi SW of Blue Tank, 4.1 air mi E of summit of Robbers Roost Mt, on Caldwell Ranch, between Madera Canyon and Bicycle Canyon, crevices of rhyolite on vertical palisade rimrock walls at top of slope on NW side of ridge (divide) ca. 6250-6280 ft, 13 Aug 2000, *Carr 19141* (TEX); N slope and summit of Mt. Livermore, rock crevices on cliffs, 29 Jul 1946, *Correll 13540* (NY, SMU); Buffalo Trail Scout Camp, Aguja Canyon, ledges 7 Aug 1966, *Correll 33350* (LL, NY, SMU); summit of Livermore Peak, 9-12 Jul 1921, *Ferris & Duncan 2595* (NY); N cliffs, Mt. Livermore, 7800 ft, 5 Aug 1925, *Hinckley 70* (NY); cliffs on N side of Timber Mtn, near Madera Springs, 6000 ft, 24 Jul 1949, *Hinckley 196* (SMU); Little Aguja Canyon, crevices in cliffs, 1495 m, 12 Jun 1931, *Moore & Steyermark 3071* (NY, PH, UC); upper canyon Limpia Creek, dry rocky ground, 10 Jun 1926, *Palmer 30660* (NY); W side of Sawtooth Mountain, rocky slopes and ledges, 4 Aug 1926, *Palmer 31955* (TEX); porphyritic cliffs of Mt. Livermore, clefts of rock, 2300 m, 6 Jun 1928, *Palmer 34363* (PH); above Madera Spring, N slopes of Timber Mtn, frequent in igneous soil, 6000 ft, 20 Jul 1947, *Warnock 6495* (SMU); Davis Mts, 13 Sep 1918, *Young s.n.* (UC). Presidio Co.: **Chinati Mts**: S side of Chinati Peak, crevices of igneous rock ledges, ca. 6900 ft, 7 Jun 1977, *Butterwick & Lott 3788* (TEX); Horse Creek Canyon on NE slope of Chinati Peak,

rock ledges at upper elevations, ca. 7000 ft, 22 Jul 1942, *Hinckley 2563* (NY, SMU); Chinati Peak, N-facing bluffs under summit, 2280 m, 21 Jul 1945, *McVaugh 7463* (LL, SMU); Chinati Peak and canyons N and E of the peak, canyon wall, rock crevices, 7 Jun 1977, *Powell 3099* (LL).

Figure 182. *Heterotheca viscida*, Cochise Co., Arizona. *Bingham 2658* (ASU).

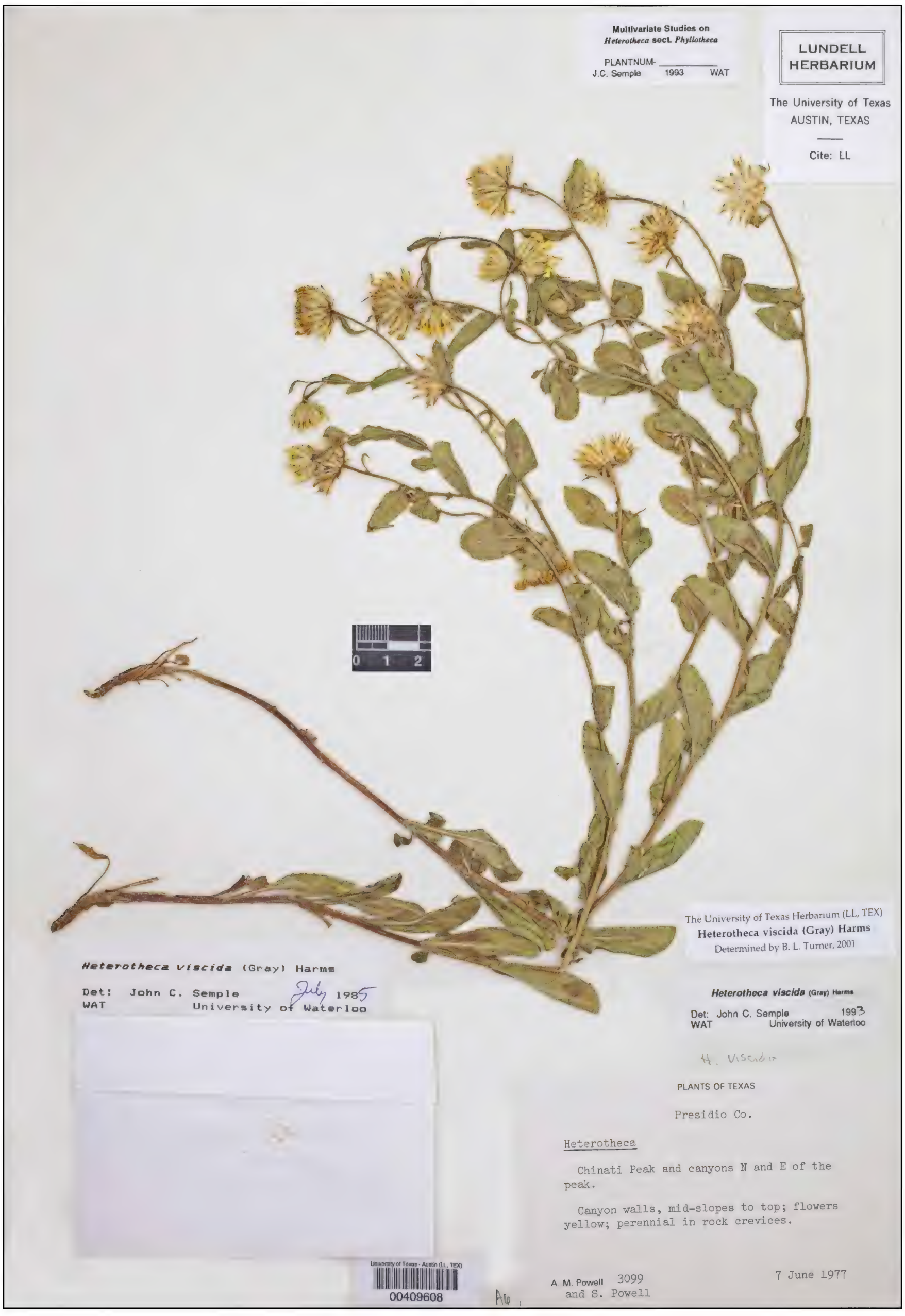


Figure 183. *Heterotheca viscida*, Presidio Co., Texas. *Powell 3099* (LL).

Figure 184. *Heterotheca viscida*, Jeff Davis Co., Texas. *Correll 33760* (LL).

Figure 185. *Heterotheca* aff. *viscida*, Socorro Co., New Mexico. *Spellenberg 10597* (ID). Variant with unusually small heads and slightly out of expected geographic range. The label says Otero Co. but the Mockingbird Mts. are in the SE corner of Socorro County.

38. HETEROTHECA KOMAREKIAE Nesom, **sp. nov. TYPE**: **Colorado**. Archuleta Co.: Quartz Creek Trail, narrow canyon of loose, highly erodable volcanic tuff, 9600 ft, large clumps, very green & leafy, gummy, 13 Aug 1994, *S. Komarek 437* (holotype: FLD, Fig. 187).

Distinctive in its rhizome-like caudex branches, nearly strictly erect stems, primarily stipitate-glandular vestiture, otherwise sparsely hispid-hirsute with a few non-glandular hairs (the whole plant with a dark green aspect), oblong-oblanceolate to elliptic or elliptic-oblong, epetiolate midcauline leaves, solitary heads on short, bracteate peduncles from upper leaf axils, and narrow ray ligules.

Herbaceous perennial, apparently somewhat colonial from rhizomes or rhizome-like caudex branches; stems and leaves dark green, stipitate-glandular and otherwise sparsely hispid-hirsute with a few non-glandular hairs. **Stems** erect, 12–30 cm tall, unbranched up to the inflorescence. **Leaves** all cauline, proximal (on rhizome branches) scale-like, largest at midstem and above, 1.5–3.5 cm long, oblong-oblanceolate to elliptic or elliptic-oblong, epetiolate with base rounded to truncate, sometimes slightly subclasping, proximal with more attenuate base and becoming petiolate, apex apiculate, surfaces stipitate-glandular, midvein sparsely hispid to hispid-hirsute. **Heads** solitary or 2–5 on bracteate peduncles from distal leaf axils; peduncles (axillary branches) 1.5–3.5 cm long. **Involucres** broadly campanulate, 9–14 mm wide (pressed); phyllaries in 3–4 graduate series, linear to linear-triangular, longest 8–10 mm, stramineous, narrowly keeled (raised midvein), glandular. **Ray flowers** ca. 12–20, ligules narrow.

The species is named for Sue Komarek, botanist and author of "Flora of the San Juans: A Field Guide to the Mountain Plants of Southwestern Colorado (1994). Two of the three known collections of the species were made by Sue.

Flowering Jul–Sep. Canyon in volcanic tuff at 9600 ft, probably waifs at lower elevation (7700–8200 ft) along rocky banks and gravel and sand bars of the East Fork San Juan River.

The three collections are from a small geographic area close to the border of Mineral and Archuleta counties (Map 16, Figs. 186, 210). *Heterotheca komarekiae* is distinctive in habit, leaf morphology, inflorescence, and vestiture and would not be confused with any other species from southern Colorado. In its green-glandular-viscid aspect, it is similar to *H. resinolens* (Front Range and central Colorado) and *H. cryptocephala* of south-central New Mexico but different from both in lack of capitular bracts and to *H. viscida* (southern Arizona to trans-Pecos Texas) but different in habit and leaf morphology.

In early September 2020, botanist Rich Haswell from South Fork, Colorado, surveyed along the East Fork San Juan River, including the site of *Komarek 510*, but did not encounter *Heterotheca komarekiae* — he found (pers. comm.) abundant *H. pedunculata* on the "first terrace of the river, which is flat and composed of grassy meadows and mixed conifer groves … among sandy dirt, gravel, and larger stones, sometimes alongside the road, sometimes between road and river, sometimes on the rocky slopes above the road." This suggests that plants of *H. komarekiae* from along the East Fork are ephemeral and have been established there from seeds washed down from higher elevation.

Additional collections. Colorado. Archuleta Co.: Along East Fork San Juan River, off Forest Rd 667, UTM 13, 334972, 4138707 (Wolf Creek Pass Quad: T36N R1E S5), near water's edge along N bank of river, rocky soil, 7715 ft, 26 Jul 2001, *Denslow 668* (RSA, Fig. 189). Mineral Co.: 16 mi NE of Pagosa Springs, E Fork San Juan River, 1.4 mi from Upper Quartz Ridge trailhead, T37N R2E Sec32, gravel and sand bar of riverbank, 8200 ft, 27 Sep 1995, *Komarek 510* (COLO, Fig. 188).

Figure 186. Distribution of *Heterotheca komarekiae*, Archuleta and Mineral cos, Colorado. The type is *Komarek 437* from along the Quartz Creek Trail at 9600 feet elevation. Localities along the rocky edges of East Fork San Juan River ('510' and '668') probably are of plants established from seeds washed down from higher elevation (comments in text).

Figure 187. *Heterotheca komarekiae*. Quartz Creek Trail, Archuleta Co. Holotype (FLD).

Figure 188. *Heterotheca komarekiae*. East Fork San Juan River, Mineral Co. *Komarek 510* (COLO).

Figure 189. *Heterotheca komarekiae*. East Fork San Juan River, Archuleta Co. *Denslow 668* (RSA). Many thanks to the RSA staff for the photo.

39. HETEROTHECA RESINOLENS (A. Nels.) Nesom, **comb. nov.** *Chrysopsis resinolens* A. Nels., Bull. Torrey Bot. Club 28: 232. 1901. **TYPE**: **Wyoming**. Albany Co.: Laramie Peak, moist mountain valleys, 13 Jul 1900, *A. Nelson 7583* (holotype: RM!; isotypes: C, COLO, CM, GH, ILL, MIN, MO!, NEB, NY, OSC, RENO, RM!, US). Images of all types! Protologue: "Open slopes in the foothills of Laramie Peak."

Chrysopsis amplifolia Rydb., Bull. Torrey Bot. Club 31: 648. 1904. *Chrysopsis foliosa* var. *amplifolia* (Rydb.) A. Nels. in Coult. & Nels., Man. Bot. Rocky Mts., 493. 1909. *Heterotheca fulcrata* var. *amplifolia* (Rydb.) Semple, Univ. Waterloo Biol. Ser. 37: 74. 1996. **TYPE**: **Colorado**. [Boulder Co.]: Plains and foothills near Boulder, Longmont, Jul 1902, *E. Tweedy 4898* (holotype: NY image!; isotypes: RM! image!).

Chrysopsis caudata Rydb., Bull. Torrey Bot. Club 31: 648. 1904. **TYPE**: **Colorado**. [El Paso Co.: Pike's Peak,] Ruxton Dell, 2950 m, 2 Aug 1901, *E.E. & E.S. Clements 143* (holotype: NY image!; isotypes: DS image!, GH image!, MIN image!, MO! image!, NEB image!, RM! image!, US image!).

Heterotheca resinolens in typical form, over its whole range, is distinctive in its erect habit, green aspect (surfaces are sessile-glandular with little other vestiture), relatively large, sessile, oblong to oblong-obovate cauline leaves, and large capitular bracts.

Semple recognized the distinctiveness of this entity, as he mapped these plants in Colorado as *Heterotheca fulcrata* var. *fulcrata* and *H. fulcrata* var. *amplifolia*, showing the two almost exactly congruent in range in Colorado and Wyoming (symbols in Wyoming outside of Albany Co. in Semple's Fig. 28 perhaps represent *Chrysopsis resinolens* var. *ciliata*, which is treated here as *H. hirsuta*, a separate species). He placed *Chrysopsis resinolens* as a synonym of var. *fulcrata*, *Chrysopsis caudata* as a synonym of var. *amplifolia*. From from his annotations and published comments, his identifications between the two varieties was based on their density of vestiture. "Variety *amplifolia* is similar in most ways to var. *fulcrata* but the leaf indument is densely short-strigose (50-200 hairs/mm2) with very few or no glands rather than sparsely to moderately hispid-strigose and glandular. It shows the same range in leaf shape that occurs in var. *fulcrata*" (1996, p. 75).

Vestiture variation in some populations of *Heterotheca resinolens* may be within the nature of the species or may indicate genetic influence from some other species, particularly *H. pumila*.

* Plants of the *Chrysopsis amplifolia* type (*Tweedy 4898*) have typical habit and leaf shape for *H. resinolens*; leaf and bract vestiture is sparsely strigose and sparsely glandular.

* The 7 or perhaps 8 plants of the type gathering of *Chrysopsis caudata* (*Clements 143*) all are erect and with large, oblong leaves and bracts, but the vestiture is variable. The US plants are glandular with little other vestiture (like the type of *C. resinolens*); those of GH, MIN, and NY are moderately strigose and apparently eglandular; those of CAS, MO, and NEB/RM (this apparently 1 plant divided at the base) are sparsely strigose and apparently eglandular or sparsely and minutely glandular (like the type of *C. amplifolia*).

Heterotheca resinolens and *H. pumila* can be similar in aspect, and hybridization and introgression may occur where their elevational ranges come into contact. Apparent hybrids occur in Boulder, El Paso, Gilpin, Grand, and Larimer counties. The geographic range of *H. pumila* is considerably wider that that of *H. resinolens*, and outside of the range of typical *H. resinolens*, no *H. pumila* variants have been encountered that suggest influence from *H. resinolens*.

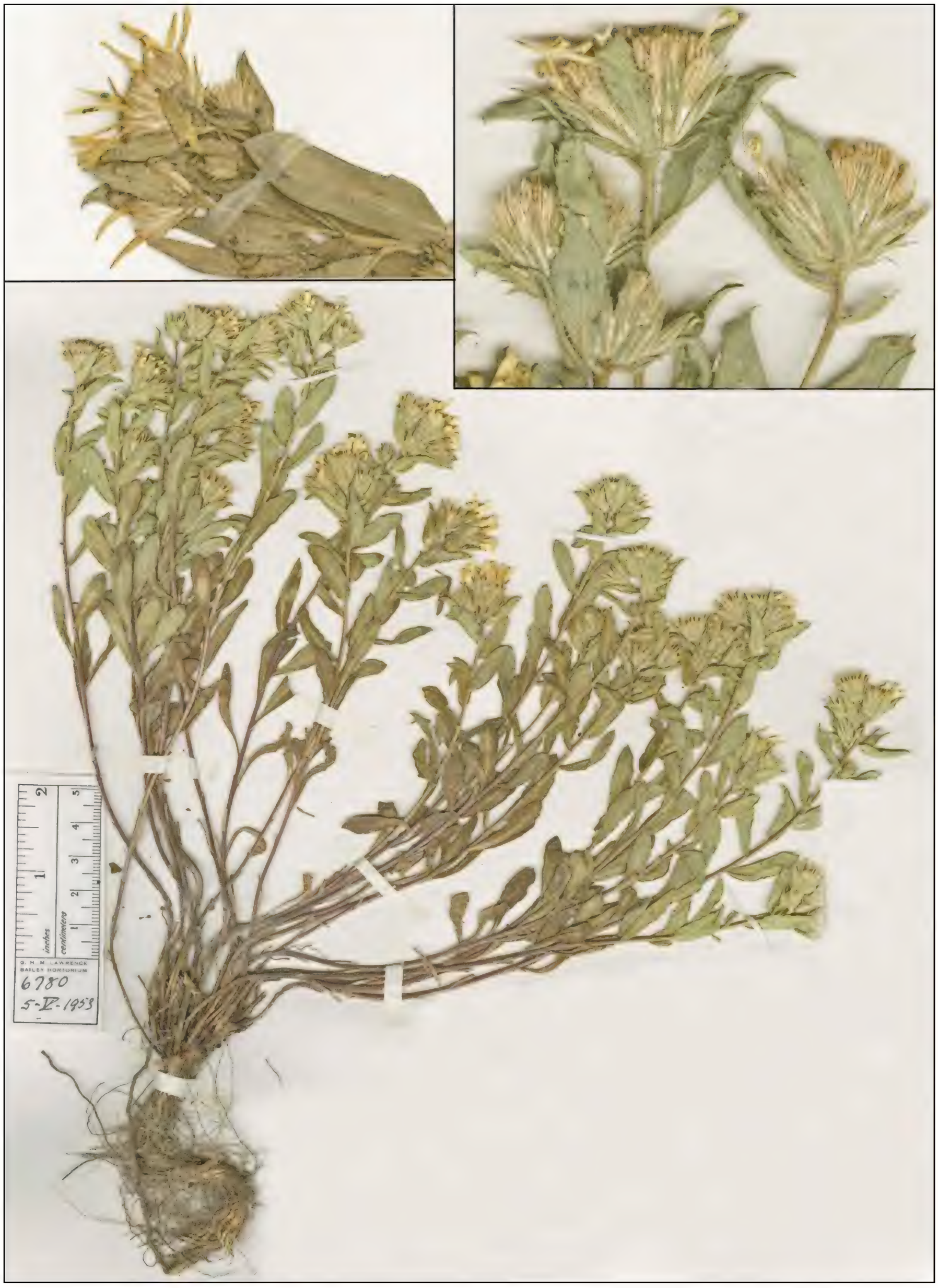


Figure 190. *Heterotheca resinolens*. Holotype (RM).

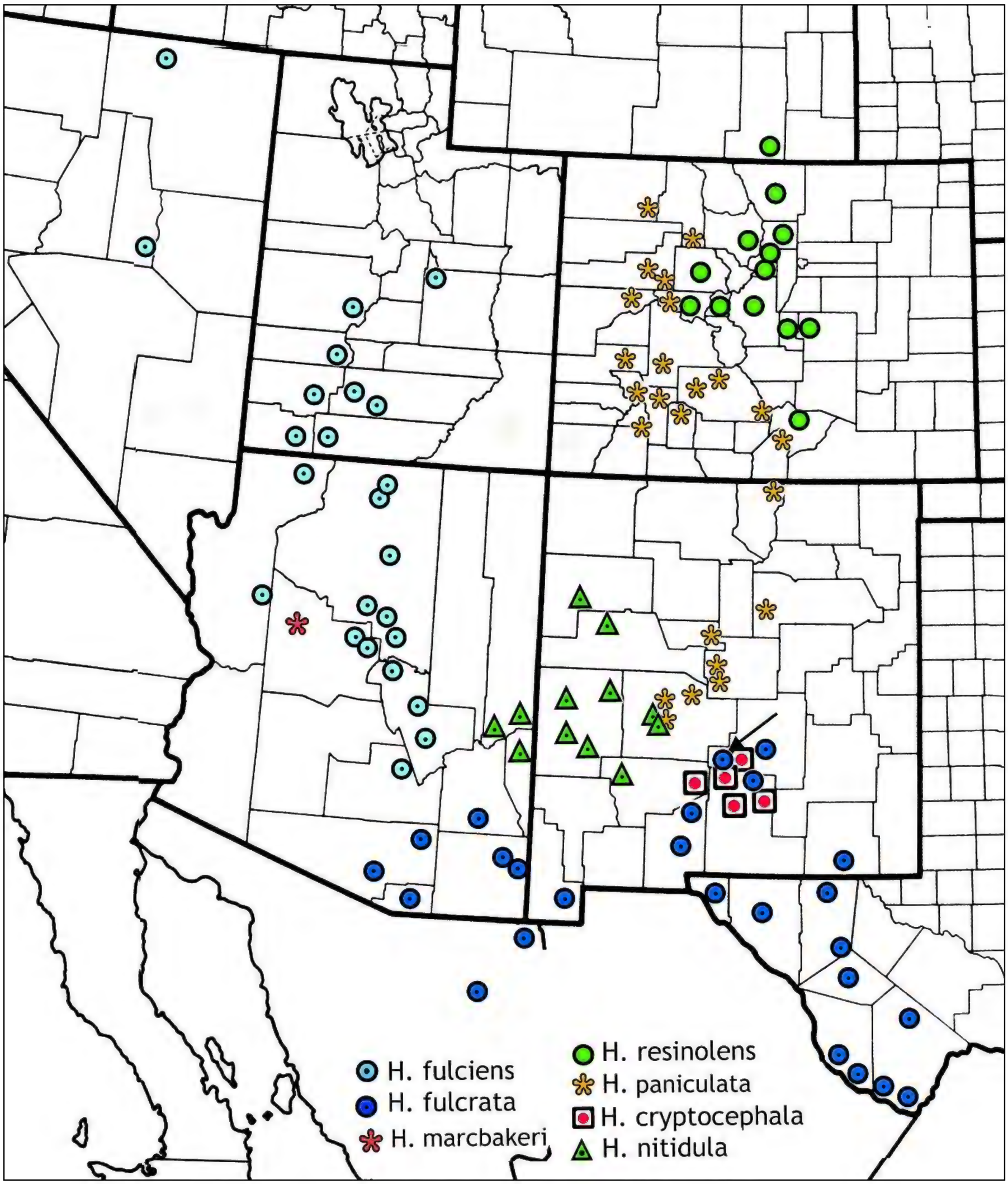


Figure 191. Distribution of *Heterotheca* species. Arrow points to type locality of *H. fulcrata* (Lincoln Co., New Mexico). See Fig. 235 for distribution of *H. fulcrata* in Mexico (Coahuila).

40. HETEROTHECA PANICULATA Nesom, **nom. nov.** *Chrysopsis floribunda* Greene, Pittonia 3: 101. 1896 [not *Heterotheca floribunda* Benth. 1844 = *Heterotheca grandiflora*]. **LECTOTYPE** (designated here): **Colorado.** Montrose Co.: Gunnison Canyon, 27 Aug 1896, *E.L. Greene s.n.* (NDG 53915 image; isolectotype: NDG 53916, Fig. 192).

The type collection of *Chrysopsis floribunda* Greene is representative of the species but the name is a later homonym and illegitimate. *Heterotheca paniculata* is a replacement name.

Heterotheca paniculata often produces lateral branches originating from proximal and midstem nodes upward, with heads arranged in a loose panicle (from the lateral branches). Branches ascending-erect or often decumbent and sprawling or declining from rock faces. Leaves relatively small (mostly 1–2.5 cm long) with minutely glandular and otherwise sparsely hirsute surfaces and coarsely short-ciliate margins. Heads small and few-flowered, often on short peduncles, prominently subtended by capitular bracts usually no longer than the involucre.

Plants perennial from a woody taproot and caudex, with many stems arising from the caudex, often thin and wiry. **Stems** ascending-erect to decumbent or declining from the base and sprawling downward in cliffside habitat, numerous from the base, 20–50 cm, often producing many lateral branches from nodes midstem upward (from as many as 15 nodes), axillary buds (as tufts of small leaves) evident on younger plants, hirsute to spreading-ascending or loosely strigose (see comments below). **Leaves** mostly cauline (basal withered by flowering in larger plants), mostly oblanceolate-obovate to narrowly oblanceolate, narrowly oblong-lanceolate, or elliptic-lanceolate, 8–26 x 2–6 mm, entire, spreading to ascending, proximal petiolate, becoming epetiolate distally, surfaces hispid-hirsute to short-hirsute with erect to ascending hairs, prominently sessile-glandular adaxially (northern system) or on both surfaces (southern system), proximal margins and/or petioles sparsely ciliate to eciliate. **Heads** clustered distally or in a loose panicle; peduncles 2–35 mm; capitular bracts (rarely 0 in a population, 1–)3–5, linear to linear-lanceolate or narrowly oblanceolate, shorter to slightly longer than the involucre. **Involucres** 5–8 mm wide (pressed), inner phyllaries 5–7 mm long, slightly keeled, sparsely hirsute to strigose, essentially eglandular or sessile-glandular distally. **Ray flowers** 7–18, laminae 1.4–1.8 mm wide. **Chromosome numbers**, 2*n*=18 (*Mosquin 5078*-Gunnison Co.), 2*n*=36 (*Mosquin 4869*-Gunnison Co.; *Mosquin 5069*-Ouray Co.; *Semple & Heard 7799*-Mesa Co.).

Flowering (May–)Jun–Aug(–Sep). Sagebrush, oak-cherry, sagebrush-juniper with ponderosa pine, Gambel oak-Douglas fir, ponderosa pine-juniper-Douglas fir, ponderosa pine/spruce-fir, aspen-spruce, spruce-fir, dry rocky slopes, gravelly soil, granite outcrops, cliff crevices and ledges, ravines and canyon bottoms; (6000–)7000–10,000(–10,700) ft.

Through most of this study, I annotated collections of this species as "*Heterotheca asprella*," but the type collections of *Chrysopsis asprella* (*Baker 379*) as well as the similar *Chrysopsis compacta* (*Baker 608*), both from southern Gunnison Co., are closest in morphology to *H. hirsutissima*, perhaps genetically influenced by *H. paniculata*, and include plants of typical *H. hirsutissima*. The holotypes of *Chrysopsis asprella* and *Chrysopsis compacta* are plants of *H. hirsutissima* and both names are treated here as synonyms of *H. hirsutissima*. Some heads in the *Baker 379* distribution (*Chrysopsis asprella*) show a capitular bract, but others do not (CORD, MIN, UC, and VT, images!) and are identified here as typical *H. hirsutissima*. And even on branches where capitular bracts are formed, their presence is inconsistent (some heads with, some without). Stems of *C. asprella* and *C. compacta* are consistently erect to erect-ascending (as in *H. hirsutissima*).

Branching of *Heterotheca paniculata* is not evident on young plants but axillary buds usually are evident and the small heads with prominent capitular bracts are a clue to the identity of the species. The species has previously been identified as *H. pumila* and *H. fulcrata* because of the capitular bracts.

Figure 192. *Heterotheca paniculata*. Isolectotype of *Chrysopsis floribunda* Greene (NDG). This plant, with long, thin stems, was sprawling-declining in its characteristic habitat (see Fig. 201).

Figure 193. *Heterotheca paniculata*, Garfield Co., Colorado. *Vanderhorst 1913* (KANU).

Figure 194. *Heterotheca paniculata*, Gunnison Co., Colorado. *Bryant 150* (KHD).

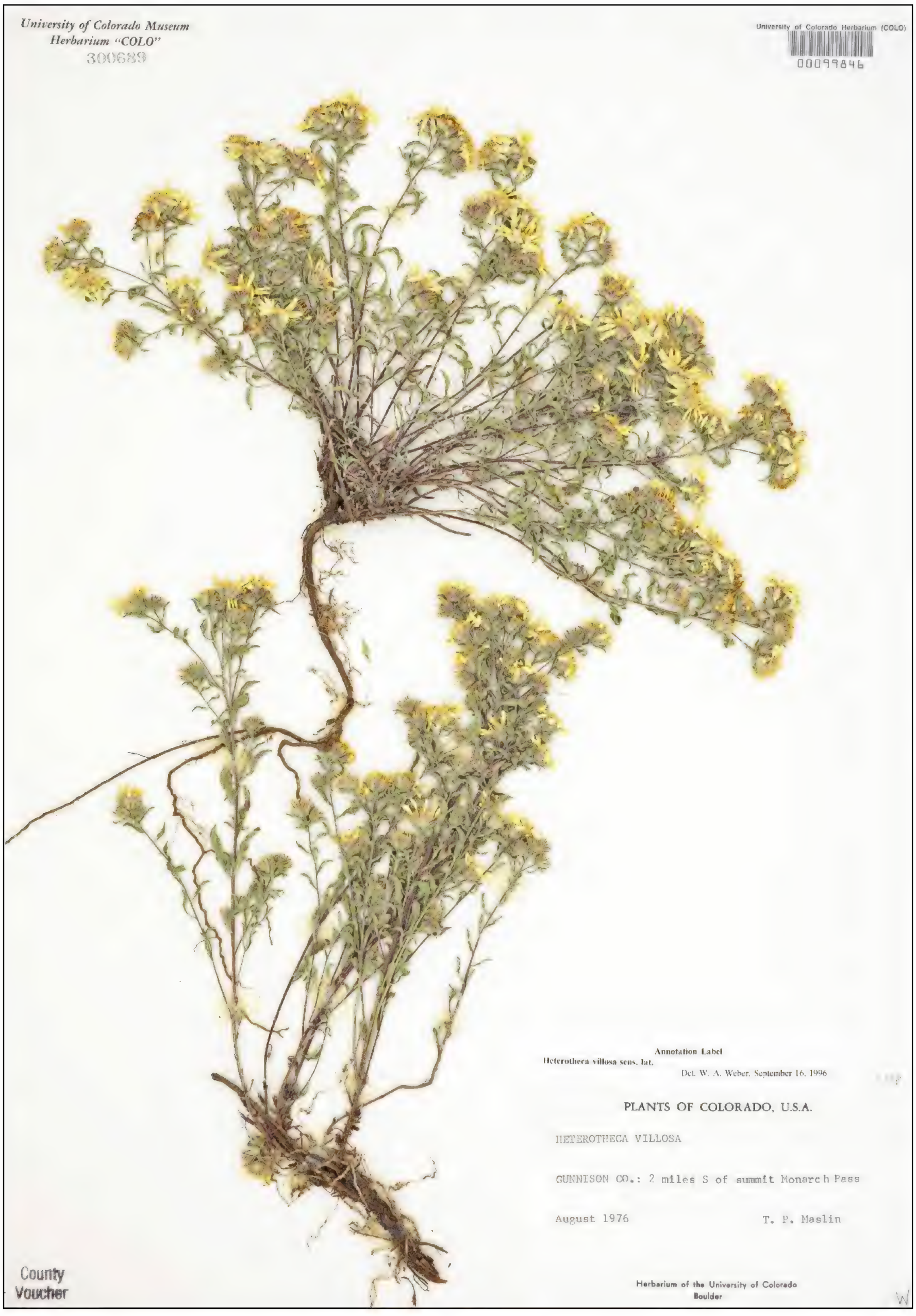


Figure 195. *Heterotheca paniculata*, Gunnison Co., Colorado. *Maslin s.n.* (COLO).

Figure 196. *Heterotheca paniculata*, Gunnison Co., Colorado. *Mosquin 4869* (COLO).

Figure 197. *Heterotheca paniculata*, Gunnison Co., Colorado. *Clark & Lederer 2242* (COLO).

Figure 198. *Heterotheca paniculata*, Gunnison Co., Colorado. *Davidson & Selkin 102* (COLO).

Figure 199. *Heterotheca paniculata*, Gunnison Co., Colorado. *Grey 664* (COLO).

Figure 200. *Heterotheca paniculata*, Gunnison Co., Colorado. *Crosswhite 1189* (RMBL).

Figure 201. *Heterotheca paniculata*. Gunnison Co., Colorado. Site of *Nesom het17-10*. Photos by Nesom, 16 Aug 2017.

Figure 202. *Heterotheca paniculata*. Hinsdale Co., Colorado, *Martin 288* (WSC).

Figure 203. *Heterotheca paniculata*. Mineral Co., Colorado. *Zeger Z-34* (FLD).

Figure 204. *Heterotheca paniculata*. Costilla Co., Colorado, *Anderson 87-104* (COLO).

Figure 205. *Heterotheca paniculata*. Socorro Co., New Mexico, *Maddux 495* (UNM).

Figure 206. *Heterotheca paniculata*. Bernalillo Co., New Mexico, *Megard s.n.* (UNM).

Figure 207. *Heterotheca paniculata*. Taos Co., New Mexico, *Holmgren 7189* (WTU).

Figure 208. *Heterotheca paniculata*. Taos Co., New Mexico. Locality of *Holmgren 7189* (Fig. 207) and *Heil 36026*. Photo by Ken Heil, July 2017.

Figure 209. *Heterotheca paniculata*. Taos Co., New Mexico, site of *Heil 36026*. Photo by Ken Heil, July 2017. Vestiture and axillary branching.

Gene flow apparently occurs where *Heterotheca paniculata* and *H. hirsutissima* are sympatric in southern Gunnison County. I studied and collected *H. hirsutissima*, apparently with influence of *H. paniculata*, on roadsides very near the type locality of *Chrysopsis compacta* (*Nesom het17-15*, 1.5 mi NE of Almont on Co. Road 742); typical *H. paniculata* (*Nesom het17-16*) occurs on cliff faces about 0.3 mile from *het17-15* and at the same elevation. I also studied and collected populations of typical *H. hirsutissima* (*Nesom het17-11*) and closely adjacent populations apparently influenced by *H. paniculata* east-northeast of Parlin (east of Gunnison) along Co. Road 76 (*het17-12*, *het17-13*). The somewhat atypical populations identified here as *H. hirsutissima* show a range of variation similar to the type collections of *H. asprella* and *H. compacta*. Obvious intermediates have not been observed where *H. paniculata* and *H. hirsutissima* are sympatric elsewhere (e.g., New Mexico).

Northern populations of *Heterotheca paniculata* (e.g., Garfield, Moffat, and Routt cos.) mostly have stems evenly and stiffly short-hirsute with deflexed hairs in a single story. Vestiture of southern Colorado populations (e.g., Gunnison, Hinsdale, Montrose, Ouray, and Saguache cos.) is more variable and some plants have loosely strigose to strongly ascending to spreading-ascending with fine hairs, some hirsute proximally but loosely strigose distally. Leaf surfaces tend to be sessile-glandular only adaxially in the north but glandular on both surfaces elsewhere.

Additional collections examined. **Colorado**. Costilla Co.: Sangre de Cristo Mts, along Hwy 160 and Sangre de Cristo Creek, 0.5 mi below turnoff of Old La Veta Pass, montane grassland on N-facing hillside, 2750 m, 22 Jul 1987, *Anderson 87-104* (COLO, Fig. 204). Garfield Co.: Glenwood Springs, 21 Aug 1918, *Osterhout 5830* (POM, RM), *5837* (RM); White River Natl Forest, Hubbards Cave, gravel soil, 8500 ft, 18 Sep 1929, *Thomson RT-77* (RM); Flat Tops/White River Plateau, East Canyon Creek, ca. 6 air mi NW of Glenwood Springs, NW-facing slope above creek, Gambel oak and scattered Douglas fir, 7200-

7600 ft, 25 Jul 1990, *Vanderhorst 1327* (RM); Flat Tops/White River Plateau, Grizzly Creek, ca. 4 air mi E of Glenwood Springs, canyon bottom with cottonwood, Doug fir, spruce, and dogwood, 6000-6200 ft, 24 Aug 1990, *Vanderhorst 1913* (KANU-Fig. 193, RM). Gunnison Co.: ca. 5 air mi SSW of Gunnison, E side of Co. Rd 32B, ca. 3.5 air mi N of Saguache County, sagebrush, 8100-8340 ft, 26 Jul 1999, *Arnett 4616* (RM); Co. Rd 25 at Willow Creek, ca. 1 air mi NW of Blue Mesa Airport, ca. 6 air mi NW of Gateview, riparian and adjacent sagebrush, 8600-8680 ft, 6 Jul 1999, *Arnett 4863* (RM); W side of Wolf Creek, ca. 2 air mi NW of summit of Nine Mile Hill, ca. 4.2 air mi SSW of Blaine Peak, ca. 11.5 air mi SE of Sapinero, sagebrush, 8440-8680 ft, 13 Jul 1999, *Arnett 5095* (RM); along Forest Rd (Uncompahgre) 861 by the Middle Fork Cimarron River, 2-3.2 air mi N of Hinsdale County, 2.8-3.6 air mi NE of Owl Creek Pass, spruce, 9200-9400 ft, 14 Aug 1999, *Arnett 7010* (RM); Uncompahgre Natl Forest, Trail 232 along Big Blue Creek, 1.6-2.1 air mi ENE of Fall Creek Falls, aspen-spruce, 9800-10,015 ft, 23 Aug 1999, *Arnett 7304* (RM); above Erikson Springs on the Kebler Pass Road, slope with *Quercus breweri* and *Prunus*, 7200 ft, 20 Jun 1971, *Breedlove 19535* (CAS); Gunnison Natl Forest, Sec 10, T15S, R87W, uncommon in subalpine park, 9200 ft, 5 Aug 1967, *Bryant 150* (KHD, Fig. 194); Curecanti Natl Rec Area, Cimarron Visitor Center exit off Hwy 50, Mesa Creek Trail along Gunnison River just below Morrow Dam, steep, S-facing slope, dry shrubland, 6835 ft, 17 Jul 2004, *Clark & Lederer 2242* (COLO, Fig. 197); near the Old Maid on Gothic Mtn, directly above Gothic Townsite, rocky soil, ca. 10,700 ft, 28 Jul 1960, *Crosswhite 1189* (RMBL, Fig. 200); R85W, T51N, high, dry, cold prairie, 8009 ft, 9 Sep 1986, *Davidson & Selkin 102* (COLO, Fig. 198); E slope of Meridian Lake, just S of drainage lock, 9200 ft, 12 Jul 1980, *Grey 295* (NY); ca. 2 mi S of Hwy 50, adjacent to Co. Road 25, cliffs S of road, 19 Aug 1980, *Grey 664* (COLO, Fig. 199); along Forest Rd 742, overlooking Taylor Park Reservoir from the south, 17 Jul 2003, *King & Garvey 12586* (NY); S. Iola, 7500 ft, 5 Jul 1961, *Hall 274* (BRY); close to Almont, 22 Jul 1968, *Harmon 1120* (BRY, DS); 2 mi W of Monarch Pass summit, Aug 1976, *Maslin s.n.* (COLO, Fig. 195); Taylor Park Dam, hard gravel overlooking water exits, 6 Aug 1962, *Mosquin 4869* (COLO-Fig. 196, DS); 7.2 mi W of Gunnison, rocky, S-facing, sage-covered slope, 16 Jun 1963, *Mosquin 5078* (DS); 32 mi E of Montrose at Blue Creek, dry slopes, 7000 ft, 17 Aug 1934, *Munz 13102* (DS, POM, TEX, UC); 2.5 mi SW of the Gunnison airport, gravelly semi-barrens, sagebrush, 8150 ft, 15 Jul 1984, *Neese 15893* (BRY, RSA); 5 mi W of Sapinero area (Blue Mesa Point) on Hwy 50, area of pinyon pine-juniper-limber pine-aspen, 8300 ft, abundant on walls and base of steep, rocky road cut, in full flower, 16 August 2017, *Nesom het17-10* (15 dups); 1.8 mi NE of Almont (jct with Hwy 135) on Co. Road 742 along Taylor River toward Taylor Park Reservoir, area of doug fir-aspen, general area of sagebrush slopes with scattered ponderosa pine, 8150 ft, scattered but common (here and on rock faces on up the canyon) on ledges and in crevices of steep rock outcrop/road cut, E side of road, 18 Aug 2017, *Nesom het17-16* (2 dups); 15.6 mi W of Gunnison, Hwy 50, red sandy soil, 30 Jun 1951, *Preece & Turner 2809* (SMU); 8 mi N of Crested Butte, base of cliffs on E face of Gothic Mtn, open cliff crevices, 10,700 ft, 28 Jul 1960, *Russell 28.6* (UC); West Elk Creek, dry rocky soil, 7460 ft, 11 Jul 1961, *Stock 423* (BRY, MO, RSA, UC); Fossil Ridge Wilderness, ca. 10.5 air mi ENE of Almont, spruce-fir, 9000-9800 ft, 3 Jul 1998, *Taylor 7917* (RM); ca. 9.5 air mi ENE of Parlin, sagebrush hills, 8850-9200 ft, 24 Jul 1988, *Taylor 9272* (RM); ca. 4.5 air mi ESE of Parlin, granite outcrops, sagebrush, 8200 ft, 25 Jul 1998, *Taylor 9455* (RM); vicinity of Mount Carbon, 3000 m, 11 Jul 1910, *Tidestrom 3742* (LL); Sapinero, crevices of cañons, 1 Jun 1898, *Wheeler 508* (RM, UC); Gothic, margins of woods and along roadside, rocky slopes, 5 Aug 1937, *Wherry C3702* (PH). Hinsdale Co.: Southern Gunnison Basin, San Juan Mts, ca. 0.2 road mi E of Cebolla Campground, ca. 2.9 air mi W of Dry Lake, ca. 11.8 air mi E of Lake City along Forest Rd 788, steep S-facing slopes and gullies of narrow canyon to an open aspen/mixed conifer forest to a rocky S-facing slope, 9320-10,000 ft, 14 Jul 1998, *Arnett 1524* (RM); near top of Slumgullion Pass, 9 Aug 1979, *Heil NCC-S 1022* (SJNM); Middle Fork Piedra River, FS Road 636, Trail 589 N of trailhead, limestone, 9000 ft, 16 Aug 1997, *Heil 11,369* (SJNM); Gunnison Natl Forest, William Creek Campground [S of Williams Creek Reservoir], campsite #7, dry grassy community, sandy & gravelly soil, 2926 m, 10 Jul 1971, *Martin 288* (WSC, Fig. 202); Cathedral, 1 mi S jct Pinos-Cebolla Rd, where road crosses Cebolla Creek and enters canyon, around cabin and 160 acres of Bob and Scottie Willey, T44N R2W sec12 NE 1/4, dry slopes and lower cliff faces along S-facing metamorphic cliff band above Cebolla Creek, dry scrub vegetation dominated by rabbitbrush, sage, and gooseberry and unique species in cracks in cliff face, 8995 ft, just beginning to bloom, 6 Jul 2010, *Williams 2010-0144* (RMBL). La Plata Co.: San Juan Natl Forest, ca 18 mi. SE of Silverton, S side of Turret, Animas River drainage fir, gravel scree slopes, 12,200 ft, 8 Aug 1961,

Michener 22 (COLO). Mesa Co.: 7.1 km E of Mesa (State St.) on Colo Hwy 65, 8000 ft, dry roadside ditch, 8 Sep 1985, *Semple & Heard 7799* - 2*n*=36 (MO). Mineral Co.: Rio Grande Natl Forest, ca. 1.5 mi N of Creede of Rd 503, igneous rock, montane community, 9450 ft, 29 Jul 1989, *Heil 5529* (SJNM); ca. 6 mi S of Wagon Wheel Gap, Rio Grande Natl Forest, private property (Humphreys Ranch) surrounding Lake Humphreys and Hay Press Lake, spruce-aspen forest below earthen dam separating lakes, along a narrow, wet channel coming from Hay Press Lake and emptying into Lake Humphreys, 9128 ft, 19 Aug 2013, *Regensberg 1437* (KHD); San Juan Natl Forest, San Juan (Rainbow) Hot Springs along the W Fork San Juan River, weedy place, 9100 ft, 27 Jun 2002, *Rink 2127* (SJNM); Wasson Ranch, near Creede, valley, 8840 ft, 29 Jul 1938, *Stewart 1136* (COLO); Wasson (near Creede), North Creek Canyon, ca. 9000 ft, 18 Aug 1939, *Stewart 1515* (COLO); San Juan Natl Forest, last park up Middle Fork [Piedra River] before entering canyon, no slope, deep sand soil, river bank with *Aster* and *Erigeron*, fairly abundant in fairly dry sites, 8500 ft, 15 Aug 1935, *Zeger Z-34* (CS, FLD-Fig. 203). Moffat Co.: Williams Fork River [tributary of Yampa River], 24 Jul 1939, *Zobel s.n.* (CAS). Montrose Co.: Montrose, 4 Jun 1901, *Baker 15* (POM); Black Cañon, 7000 ft, 1 Aug 1901, *Baker 684* (DS, MO, NY, POM, RM-3 sheets, UC-2 sheets); Black Cañon of the Gunnison, 7000 ft, 22 Aug 1896, *Crandall s.n.* (RM); felsige abhinge, Black Cañon, 7300 ft, Sep 1893, *Purpus 710* (UC). Ouray Co.: N-facing hillside, just S of and overlooking Ouray, 16 Jun 1963, *Mosquin 5069*, voucher for 2n=18II (COLO). Pitkin Co.: 2 mi W of Aspen dry meadow, 8000 ft, 19 Jul 1952, *Green 422* (PH). Routt Co.: Park Range, ca. 16.5 air mi SE of Yampa, ca. 4 air mi NNE of McCoy, in canyon along Rock Creek, sagebrush slope, 7300 ft, 8 Aug 1989, *Nelson 17885* (RM). Saguache Co.: ca. 0.1 road mi W of Colo Hwy 114 on BLM Road 3074, ca. 3.6 air mi ESE of Cooper Mtn, sagebrush ravine, 8390-8410 ft, 28 Jul 1999, *Arnett 5759* (RM); Great Sand Dunes Natl Monument, Castle Creek, 8400 ft, 19 Jul 1951, *Bean 51-82* (COLO); Medano Canyon, ca. 2 mi E of Great Sand Dunes NM, along road in canyon bottom, aspen, 9000 ft, 23 Sep 1973, *Dixon 2242* (ALAM); Wet Mts, Wet Mtn Valley, Cochetopa Hills, Soda Spring Gulch, Co. Rd LL56, ca. 7 air mi WSW of Villa Grove, igneous outcrops and adjacent grassland, 8600-9400 ft, 31 Jul 1999, *Hartman 65518* (RSA); ca. 5 mi S of Poncha Spgs on US Hwy 24 to Marshall Pass Rd, ca. 1 mi E of Marshall Pass at base of Mt Ouray, ca. 2 mi SW of summit, 11,500 ft, 4 Sep 1993, *Heil 8097* (SJNM); Hwy 114, 10.2 mi S of jct with Hwy 50, S of Parlin, E of Gunnison, sagebrush hills with scattered doug fir-ponderosa pine-doug fir-juniper, 8200 ft, abundant on ledges and in crevices of steep rock wall, E side of hwy, 17 Aug 2017, *Nesom het17-14* (10 dups); Gray's (E of Marshall Pass), 26 Aug 1910, *Tidestrom 4080* (MO); 4.5 mi up SE slopes of road leading to Marshall Pass, roadside, ponderosa pine/spruce-fir ecotone, 17 Jul 1991, *Turner 15999* (TEX). **New Mexico**. Bernalillo Co. [Sandia Mts]: Sandia Crest, open rocky ground, 10,400 ft, 15 Aug 1966, *Bennett 8787* (BRY); Sandia Crest, open meadow near Kiwanis cabin, 10,500 ft, 30 Sep 1956, *Megard s.n.* (UNM-2 sheets digital images!, Fig. 206). San Miguel Co.: Las Vegas, Upper Gallinas Creek, 2200-2700 m, 9 Jun 1926, *Arsene 17559* (LL). Socorro Co.: Along Cañon del Alamito, N side of Ladrons [Ladrón Peak], 6200 ft, *Baca 190*; 6500 ft, *Baca 236* and *269*; 7400 ft, *Baca 267* (all UNM digital images!); Sevilleta Wildlife Refuge, Los Pinos [Mts], W face behind Nunn/Burris windmill, 5700-6800 ft, 25 Jun 1991, *Maddox 495* (UNM, Fig. 205); Royal Canyon [in low mtns between San Antonio and Magdalena Mts], 5 mi W of San Antonio, cliffs and cliff base, 23 Jun 1982, 5200 ft, *Wahl 77* (UNM digital image!). Taos Co.: Ca. 7 mi E of Amalia, County Road 1950 just N of Costillo Creek, talus slope, S-facing slope just E of gauging station and cattle guard, 8495 ft, Jul 2017, *Heil 36026* (SJNM and 7 dups); Sangre de Cristo Mts, Costilla Creek, 7.8 mi (6 airline mi) SE of Amalia [Hwy 196], common in open rocky areas, 8500 ft, 15 Aug 1973, *Holmgren 7189* (BRY!, NMC!, WTU-Fig. 207); Carson Natl Forest, Forest Service Rd 1950, 0.7 mi E of forest boundary, Costilla Creek, mixed coniferous forest, 8900 ft, 17 Jul 2017, *O'Kane 9962* (SJNM). Torrance Co.: Manzano Mts: New Canyon Campground, ca 5 mi E of Manzano, mixed conifer forest with *Abies*, *Pinus ponderosa*, and *Quercus*, 7500 ft, 21 Aug 1995, *Allred 6281* (BRY, NMCR-not seen, NY); Capilla Peak, meadow, 9300 ft, 23 Jun 1963, *Bedker 1063* (UNM digital image!); Manzano Peak vicinity, 10,000 ft, 18 Jun 1962, *Bedker 683* (UNM digital image!); crest near Manzano Peak, 9900 ft, 18 Aug 1962, *Bedker 687* (UNM digital image!); Colorado (Red) Canyon, 1.5 mi W of Red Canyon Camp, ponderosa pine-doug fir, 8900 ft, 3 Aug 1963, *Bedker 1298* (UNM digital image!); Trigo Canyon, 1/4 mi E of Kennedy Camp, pinyon-juniper, 6400 ft, 2 Sep 1963, *Bedker 1544* (UNM digital image!).

41. HETEROTHECA PUMILA (Greene) Semple, Brittonia 39: 383. 1987. *Chrysopsis pumila* Greene, Erythea 2: 95. 1894. **TYPE**: **Colorado**. [Clear Creek Co.]: Upper Bear Creek, Jul 1889, *E. Greene s.n.* (holotype: NDG 53930 image!). Protologue: "Middle Colorado, high mountains toward the headwaters of Bear Creek."

Chrysopsis cooperi A. Nels., Bot. Gaz. 40: 63. 1905. **TYPE**: **Colorado**. [Boulder Co.]: Long's Peak, near timberline, 3 Aug 1904, *W.S. Cooper 50* (holotype: RM! image!; isotype: MIN image!).

Chrysopsis alpicola Rydb., Bull. Torrey Bot. Club 31: 649. 1905. **LECTOTYPE** (Semple 1987): **Colorado**. [Jackson Co.]: Clark's Peak, 11,700 ft, 1 Aug 1896, *C.F. Baker s.n.* (NY 163220; isolectotypes: MO!, NDG, NY 163178). The NDG label is marked as Baker #19.

Chrysopsis alpicola var. *glomerata* A. Nels., Bot. Gaz. 40: 64. 1905. **TYPE**: **Colorado**. Larimer Co.: Estes Park, Long's Peak House, 9000 ft, Aug 1904, *W.S. Cooper 174* (holotype: RM!; isotype: MIN image!).

Semple annotated the MIN isotype in 1997 as *H. pumila* but in publication (1996, 2006) placed *C. alpicola* var. *glomerata* as a synonym of *Heterotheca villosa* var. *foliosa*.

Plants taprooted, sometimes with rhizome-like caudex branches. **Stems** mostly 10–30(–35) cm, ascending-erect to decumbent-ascending, hirsute to villous-hirsute, glandular. **Leaves** oblong to oblanceolate, lower leaves subpetiolate, often becoming sessile distally, strigose-hirsute to pilose-strigose or loosely strigose-villous with ascending hairs, glandular, petiole and proximal margins usually spreading-ciliate, mostly even-sized to the heads. **Heads** solitary or less commonly clustered on short distal branches; capitular bracts longer than the involucre, oblong to oblanceolate or narrowly elliptic-lanceolate. **Involucres** 10–15 mm wide (pressed); phyllaries in 3–4 series weakly graduate in length, linear-lanceolate with acute to acuminate apices and thin-scarious margins, hirsute to hirsute-villous and characteristically with long, fine hairs, glandular,. **Chromosome numbers** (Semple 1996, p. 85): "2*n*=18, a few reports; 36, about a dozen reports);" and (p. 86) "the few diploids known are atypical with smaller heads and a more *minor*-like reduction in upper leaf size."

Heterotheca pumila occurs abundantly in subalpine and alpine habitats at (7500–)9000–12,100 feet on rocky slopes, scree slopes, alpine meadows, and roadsides and roadbanks; occurrences at lower elevations usually are with ponderosa pine and douglas fir; records below that perhaps show genetic influence of other species, especially along the Front Range. It is known only from Colorado and closely adjacent Carbon Co., Wyoming, and Taos Co., New Mexico. Plants noted and mapped by Semple (1996) as "aff. *H. pumila*" in the Abajo and La Sal Mountains of Utah are identified in the present study as *H. pedunculata*. Apparently emphasizing the occurrence of prominent capitular bracts, Semple (1996, p. 86) noted that *H. pumila* "appears to be a higher elevation race of the fulcrata complex close to the narrow-leaved *resinolens* morph of *H. fulcrata* var. *fulcrata*."

New Mexico. Taos Co.: Culebra Range, Vermejo Park Ranch, steep E-facing bowl 1.2 air mi S of Big Costilla Peak and 0.1 air mi E of point 12931, steep talus, scree, and rock slopes, low alpine vegetation with *Trifolium attenuatum*, *Penstemon whippleanus*, *Geum rossii*, and *Carex*, 12,542 ft, 21 Jul 2007, *Legler 6359* (RM!; documentation of state distribution record by Legler 2010).

Wyoming. Carbon Co.: Sierra Madre, S slope of Quartzite Peak, ca 0.3 mi NW of Wyo Hwy 79 and 13.5 mi WSW of Encampment, 14 Jul 2001, *Fertig 19710* (RM); Sierra Madre, Bridger Peak, 24 Aug 1903, *Goodding 2010* (RM); Medicine Bow Mts, Kennaday Peak, ca 15 air mi E of Saratoga, 2 Sep 1984, *Hartman 19822* (RM); Battle Mtn, outcrop on Battle Pass on Hwy 70, 9916 ft, 25 Aug 1995, *Semple & Zhang 10412* (MO). Larimer Co.: Summit of North Park Range, rocky ledges, 10 Aug 1903, *Goodding 1826* (PH-2 sheets).

Heterotheca pumila is variable in habit, stem length, vestiture, and development of capitular bracts — even when in high-elevation habitats apparently apart from genetic influence of other goldenaster species. Hybrids apparently occur with *H. resinolens* (see comments below), *H. hispida*, and others. Variants with elongate (bracteate) peduncles and reduced capitular bracts occur in Garfield, Grand, and Larimer counties, at 7800-8200 ft elevation, where it is possible that *H. hirsutissima* may be involved in the genetics. Because of its capitular bracts, *H. paniculata* sometimes has been identified

as *H. pumila*, but *H. paniculata* has smaller heads that tend to be distally clustered (shorter peduncles), shorter capitular bracts, short-hirsute stems and leaves, and it occurs in drier habitats at lower elevations.

The distinction of *Heterotheca schneideri* from typical *H. pumila* was recognized late in the study and my annotations of the southwestern population system (here as *H. schneideri*) have been mostly as *H. pumila*.

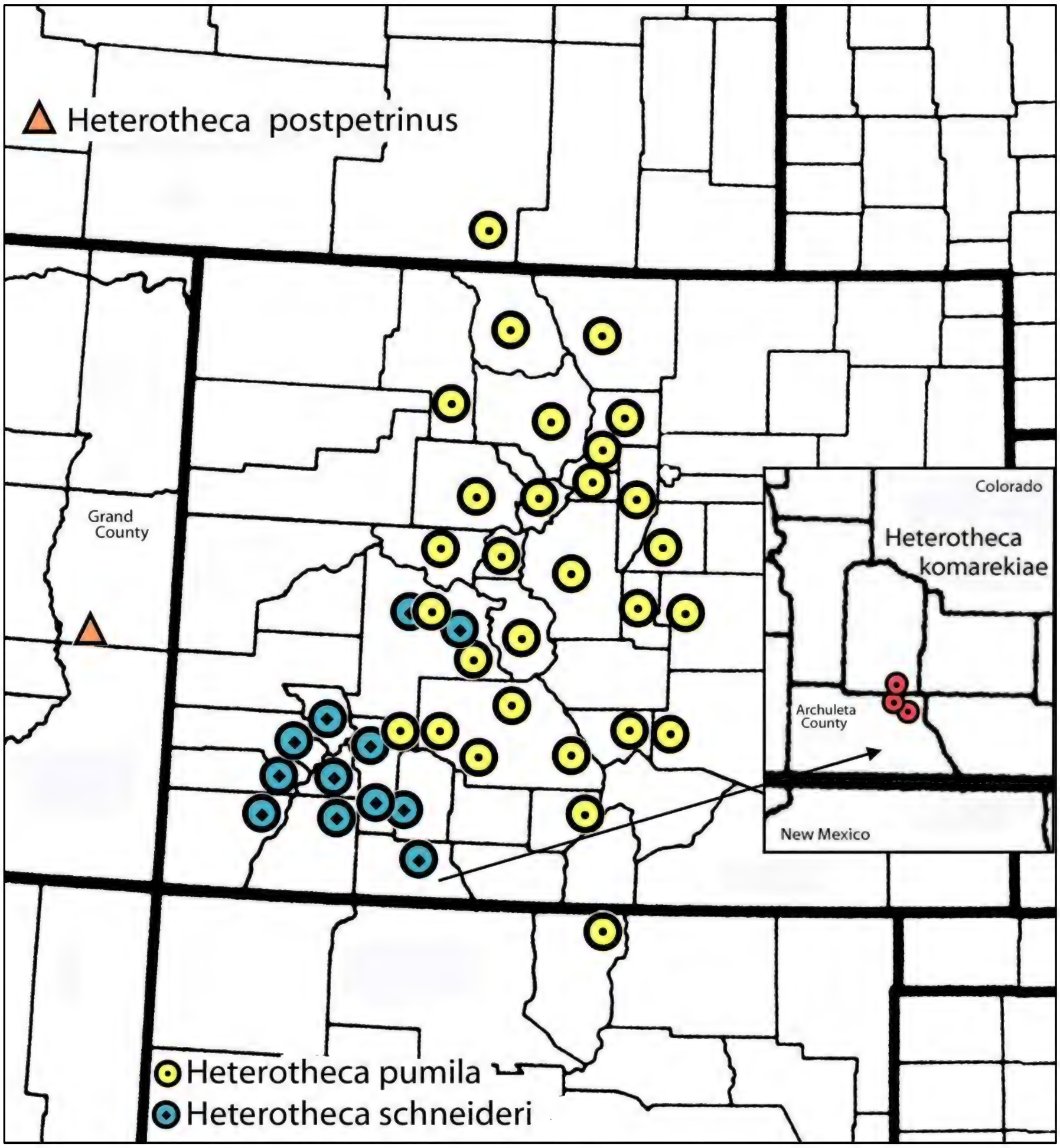


Figure 210. Distribution of *Heterotheca pumila*, *H. schneideri*, *H. postpetrinus*, and *H. komarekiae*. *Heterotheca schneideri* is essentially endemic to the San Juan Mountains (it probably occurs in southwestern Gunnison Co. and two collections document it from the Sawatch Range of central Gunnison Co.). *Heterotheca pumila* reaches the San Juan Mountains at the southwestern corner of its range in Saguache and Hinsdale counties.

Figure 211. *Heterotheca pumila*, Gunnison Co., Colorado, Kebler Pass Road, ca. 2.5 mi W of Crested Butte, locality of *Nesom het17-17* (BRIT). Taprooted, not colonial but spreading habit through rhizome-like proximal stems or caudex branches. Photos by Nesom, 18 August 2017.

Figure 212. *Heterotheca pumila*. Holotype of *Chrysopsis pumila* Greene (NDG).

Figure 213. *Heterotheca pumila*. Details from *Chrysopsis pumila* holotype (NDG).

Figure 214. *Heterotheca pumila*. Top: Details from *Chrysopsis pumila* holotype (NDG). Bottom: Details from *Chrysopsis cooperi* holotype (RM).

Figure 215. *Heterotheca pumila*. Detail from *Chrysopsis alpicola* lectotype (NY).

Figure 216. *Heterotheca pumila*. Variation in involucral morphology; heads from collections from various localities. Compare with heads of *H. schneideri* in Fig. 227.

Figure 217. *Heterotheca pumila*. Clear Creek Co., Colorado. *Smookler 272* (KHD).

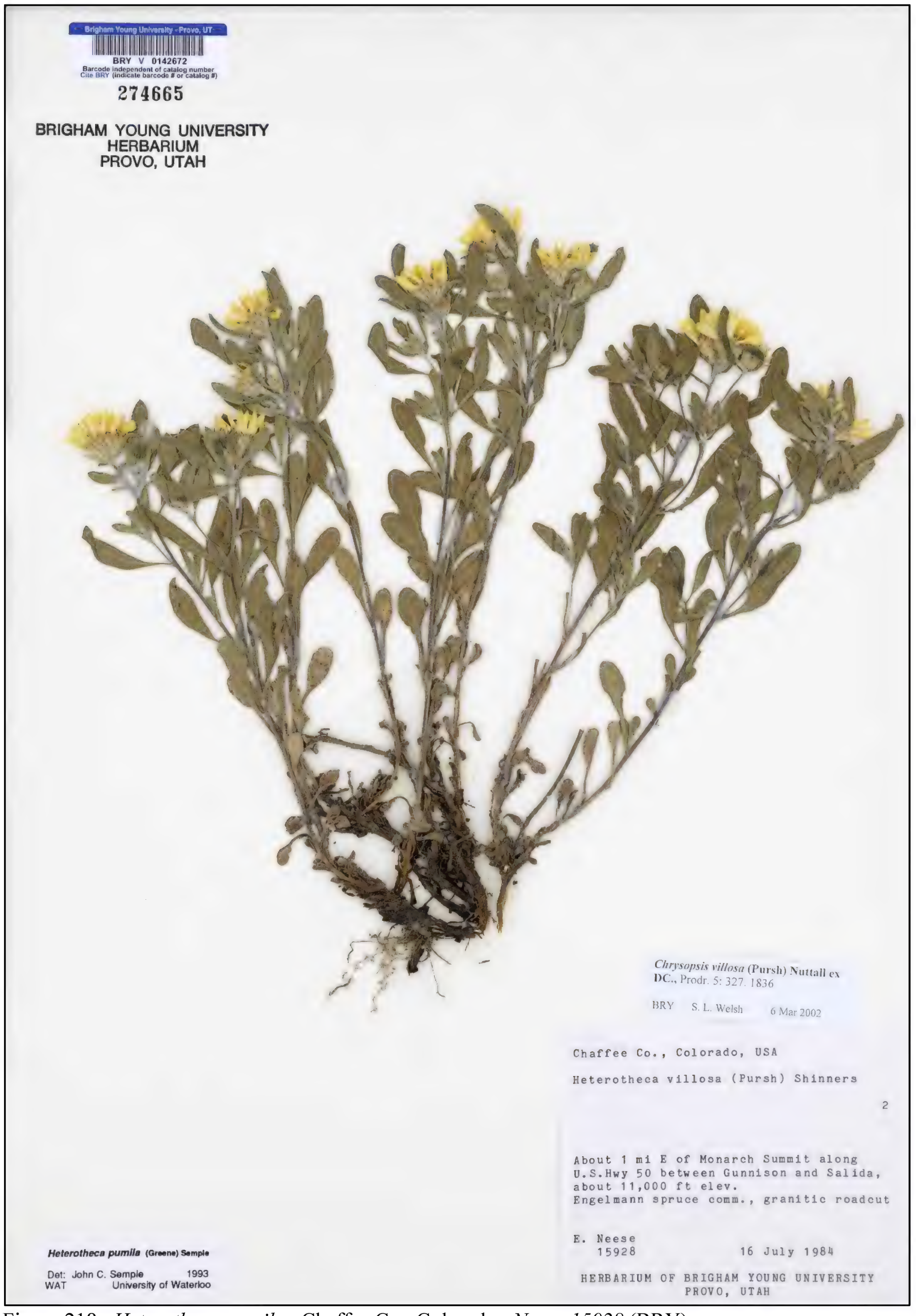


Figure 218. *Heterotheca pumila*. Chaffee Co., Colorado. *Neese 15928* (BRY).

Figure 219. *Heterotheca pumila*. Park Co., Colorado. *Hogan 2837* (KHD).

Figure 220. *Heterotheca pumila*. Summit Co., Colorado. Stems and leaves hirsute to villous-hirsute. *Nelson 725* (BRY).

Figure 221. *Heterotheca pumila*. Summit Co., Colorado. *Harms 2089* (KANU). Stems and leaves loosely strigose, and leaf margins mostly without marginal cilia, an uncharacteristic vestiture for the species, more like *H. schneideri*. Compare with Fig. 220 from Summit Co., which has typically villous-hirsute to strigose-villous vestiture.

Figure 222. *Heterotheca pumila*. Saguache Co., Colorado. *Mooers 397* (NY).

42. HETEROTHECA SCHNEIDERI Nesom, **sp. nov. TYPE**: **Colorado**. La Plata Co.: La Plata Mts, road from La Plata to Eagle Pass, 10,600 ft, roadside weed, 1 Aug 1963, *T. Mosquin 5429* with J.M. Gillet, voucher for chromosome count of 2*n*=36, as " Heterotheca pumila" (holotype: COLO-Fig. 231; isotype: DS).

Similar to *Heterotheca pumila* in its high elevation habitats, low, caespitose habit with evenly leafy stems and prominent capitular bracts but different in its closely short-strigose stems and leaves, more prevalent distal branching, and phyllaries more distinctly triangular, more numerous, more strongly graduate, and with thickened (vs. thin-scarious) margins.

Plants taprooted, caespitose, sometimes with rhizome-like caudex branches or basal offsets; aromatic. **Stems** 8–20 cm, erect to ascending-erect or decumbent-ascending, sparsely to moderately, loosely strigose with short hairs, eglandular or minutely glandular immediately below the heads. **Leaves** oblong to elliptic or oblanceolate, lower leaves subpetiolate, often becoming sessile distally, mostly even-sized up to the heads, midcauline 10–32 mm long 3–9 mm wide, sparsely to moderately strigose, minutely glandular adaxially, eglandular abaxially, margins eciliate or sometimes with a few spreading cilia at the petiole base. **Heads** terminal on leafy stems, solitary or loosely clustered from distal branches; capitular bracts as long or longer than the involucre, oblong to oblanceolate or narrowly elliptic-lanceolate. **Involucres** campanulate, 10–15 mm wide; phyllaries in 4–5(–6) series strongly graduate in length, narrowly triangular with acute apices and thickened margins, distinctly keeled, often with purple margins and apex, finely short-strigose to hirsutulous-puberulent, minutely glandular. **Ray flowers** 14–20, ligules 10–14 mm long. **Chromosome number**, 2n = 36 (as "*Heterotheca pumila*"): La Plata Co., *Mosquin & Gillett 5429*; Ouray Co., *Harms 2071*.

Flowering (Jun–)Jul–Sep. Open rocky and gravelly slopes, talus, meadows, aspen, spruce, pine-fir, spruce-fir, and above tree line; (8000–)9000–12,700 ft.

Named for Al Schneider of Cortez, Colorado, webmaster of *Southwest Colorado Wildflowers — Wildflowers, ferns, & trees of Colorado, New Mexico, Arizona, & Utah*, which provides a wealth of information on the regional flora. Al and his wife Betty are ardent and discriminating field botanists and photographers.

The contiguous geography and similarity in habitat of *H. schneideri* and *H. pumila* suggest that they may be most closely related to each other (especially as they have previously been considered conspecific), but *H. schneideri* is similar in vestiture and production of capitular bracts to *H. nitidula*, which also is geographically close. *Heterotheca pedunculata* lacks capitular bracts but has closely strigose vestiture and is geographically close as well. Collections from Ouray Co. (*Beaman & Erbitsh 1167*, COLO; *Underwood & Selby 338*, NY), with long, ebracteate peduncles but occasional capitular bracts, perhaps show gene exchange between *H. pedunculata* and *H. schneideri* — plants of both collections were growing below the normal elevational range of *H. schneideri* but within that of *H. pedunculata*.

1. Stems, leaves, and bracts short-strigose, leaves and bracts eciliate; phyllaries in 4–5(–6) strongly graduate series, finely short-strigose to hirsutulous-puberulent, margins thicker, not scarious ..... 42. **Heterotheca schneideri**

1. Stems, leaves, and bracts strigose-villous to villous-hirsute or hirsute, leaves and bracts spreading-ciliate to weakly ciliate; phyllaries in 3–4 weakly graduate series, hirsute to hirsute-villous and characteristically with long, fine hairs, margins thin-scarious ..... 41. **Heterotheca pumila**

Additional collections. Colorado. Archuleta Co.: San Juan Mts, Quartz Lake Trail below timberline, 6 Sep 1998, *M. Heil 59* (SJNM); San Juan Natl Forest, Nipple Mtn Rd, 2.6 mi from switchbacks sign, large road cut, 10,411 ft, 9 Aug 2002, *Heil 19,919* (SJNM). Dolores Co.: San Juan Natl Forest, East Fork Dolores River, confluence of North and South Forks of Twin Creek, East Fork Trail, ca 6.5 air mi NE

of Rico, SSW-facing slope with Engelmann spruce, scattered aspen, and *Symphoricarpos*, 10,400-10,600 ft, 13 Jul 1994, *Moore 3111* (RM); San Juan Natl Forest, ca 3 air mi N of Rico, beaver pond along Colo Hwy 145, willow thicket surrounding beaver pond and seepage, scattered blue spruce around perimeter of pond, S- to SE-facing, 9000 ft, 16 Aug 1994, *Moore 3950* (RM). Gunnison Co.: Ca. 2 mi NW of Crested Butte, *Artemisia-Salix-Populus*, 9000 ft, sandy soil, 12 Jul 1969, *Higgins 2173* (BRY, Fig. 234); ca. 2.5 air mi W of Pittsburg, subalpine avalanche meadow, 11,200-11,300 ft, 18 Aug 1998, *Taylor 10685* (COLO). Hinsdale Co.: San Juan Natl Forest, Weminuche Wilderness Area, N side of La Osa Creek ca. 1 mi W of San Juan Outfitters Camp, 10,462 ft, 9 Jul 2004, *Heil 24,252* (SJNM); San Juan Natl Forest, Weminuche Wilderness Area, ridge on W side of head of North Fork Los Pinos River, 11,758 ft, 2 Aug 2003, *O'Kane 7459* (SJNM); San Juan Natl Forest, Weminuche Wilderness Area, 1/2 mi SE of Granite Lake along the Weminuche Trail, 10,400 ft, 6 Jul 2003, *Rink 2260* (SJNM). La Plata Co.: San Juan Natl Forest, 28 mi N of Durango on Hwy 550, Purgatory Campsite, along trails under aspen woods with scattered spruce, 8 Aug 1961, *Harms 2058* (KANU, Fig. 230); San Juan Natl Forest, 11.1 mi up Middle Mtn Rd from Vallecito Rd, very large montane meadow, 10,740 ft, *Heil 20,550* (SJNM); San Juan Natl Forest, trailhead to Lime Ridge and Ruby Lake, corkbark fir and Engelmann spruce, 11,543 ft, 2 Sep 2004, *Heil 24,674* (SJNM). Montezuma Co.: Cascade Creek about 4 mi S of Purgatory Ski Resort, gravelly hillside, aspen-spruce, 8000 ft, 13 Aug 1986, *Kass 2543* (BRY, Fig. 232). Ouray Co.: 12 mi S of Ouray, 1 mi N of Red Mtn Pass on Hwy 550, steep mtn slopes, open spruce forest, 9 Aug 1961, *Harms 2071*, voucher for $2n$=36 (KANU, SASK, WAT) and *Harms 2072* (SASK). San Juan Co.: 6.5 mi S of Silverton on Hwy 550, Molas Divide, rocky hillside and meadow above, 10,900 ft, numerous in clumps, 8 Aug 1961, *Harms 2063* (KANU, Fig. 229); 2.2 mi S of Silverton on Hwy 550, granite outcroppings, open roadside in spruce forest, 8 Aug 1961, *Harms 2064* (KANU); ca. 3/4 mi S of Cascade Creek and 1/10 mi W of US Hwy 550, base of Engineer Mtn, aspen, spruce, douglas fir, white fir, 8909 ft, *Heil 19,785* (SJNM); Weminuche Wilderness, West Needle Mts, N of Crater Lake, open gravelly slope, 11,300 ft, 1 Aug 1997, *Hogan 3266* (COLO, Fig. 228); West Needle Mts, Old Lime Creek Road, near Coal Creek, dry, E-facing hillside, 9700 ft, 3 Aug 1997, *Hogan 3302* (COLO); 7 mi S of Silverton, dry rocky hillside, 10,500 ft, 13 Aug 1936, *Rollins 1544* (NY); 1.6 mi from Stony Pass Jct, talus slopes, pine-fir, 7 Aug 1992, *Thorne 15,052* (BRY, Fig. 233); San Juan Natl Forest, S slope of Coal Bank hill, ca. 9500 ft, 18 Jul 1985, *Trulove 110* (SJNM); Colorado Trail N of Little Molas Lake, North Lime Creek drainage, open area of dry drainage, 17 Aug 2002, *Wingate 7047* (KHD).

The two collections identified here as *Heterotheca schneideri* from Gunnison Co. are from an area where *H. pumila* is abundant and is the only place where the two species appear to be sympatric. Field observations and further collections are needed to clarify the biology.

Figure 223. *Heterotheca schneideri*. Dolores Co., Colorado, Calico National Recreation Trail at ca. 11,800 ft elevation. Photo by Al Schneider, 19 August 2009.

Figure 224. *Heterotheca schneideri*. San Miguel Co., Colorado, Sneffels Highline Trail. Photo by Al Schneider, 4 August 2004.

Figure 225. *Heterotheca schneideri*. Montezuma Co., Colorado, ca. 1 mile SW of the Roaring Forks Road on the shoulder of Forest Service Road 435, ca. 9900 ft elevation. Photo by Al Schneider, 5 August 2020.

Figure 226. *Heterotheca schneideri*. Above: Dolores Co., Colorado, Calico Trail. Below: Montezuma Co., Colorado, ca. 1 mile SW of the Roaring Forks Road. Photos by Al Schneider, 19 August 2009.

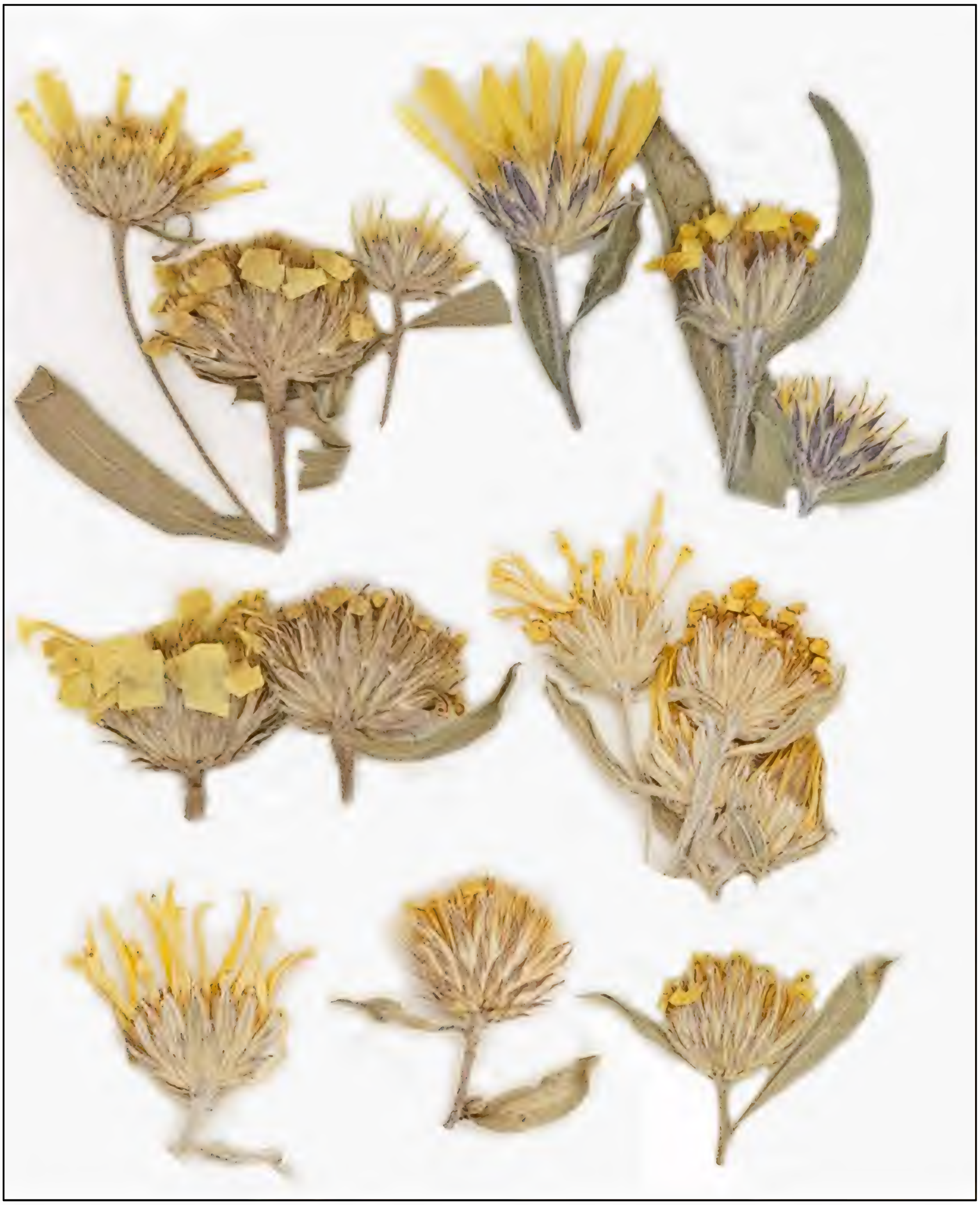


Figure 227. *Heterotheca schneideri*. Variation in involucral morphology; heads from various collections and localities.

Figure 228. *Heterotheca schneideri*. San Juan Co., Colorado. *Hogan 3266* (COLO).

Figure 229. *Heterotheca schneideri*. San Juan Co., Colorado. *Harms 2063* (KANU).

Figure 230. *Heterotheca schneideri*. La Plata Co., Colorado. *Harms 2058* (KANU).

Figure 231. *Heterotheca schneideri*. La Plata Co., Colorado. Holotype (COLO).

Figure 232. *Heterotheca schneideri*. Montezuma Co., Colorado. *Kass 2543* (BRY).

Figure 233. *Heterotheca schneideri*. San Juan Co., Colorado. *Thorne & Armstrong 15052* (BRY).

Figure 234. *Heterotheca schneideri*. Gunnison Co., Colorado. *Higgins 2173* (BRY).

43. HETEROTHECA FULCIENS Nesom, **sp. nov. TYPE: Arizona.** Yavapai Co.: Near Mormon Pocket springs along Verde River, ca. 9.6 mi NW of Clarkdale, floodplain in cobble, gravel, and sand, 1120 m, 30 Sep 2012, *F.S. Coburn 1440* (holotype: ASU!, Fig. 236).

Similar to *Heterotheca fulcrata* sensu stricto in its prominent capitular bracts but rhizomatous, leaves more elongate and more consistently eglandular, heads often more numerous in denser capitulescence (shorter peduncles), and capitular bracts less densely ciliate with shorter hairs.

Perennial, producing basal offsets and/or short rhizomes. **Stems** (1–)5–10 from an irregularly branched caudex, 5–20(–25) cm tall, hirsute to villous-hirsute with variable length (not strongly 2-storied), sometimes deflexed hairs, usually minutely glandular. **Leaves** mostly cauline (basal withered by flowering), spreading to ascending, midcauline lanceolate to oblanceolate, lanceolate-oblong, or linear-lanceolate, 12–34 x 3–8(–10) mm, length/width ratio 2.8–7/1, surfaces loosely strigose to strigose-sericeous with short hairs, sometimes very sparsely so, minutely glandular. **Heads** on paucibracteate peduncles 2–4(–5) cm long, 2–10 and compactly to loosely corymboid, rarely solitary. **Involucres** 6–9(–10) mm wide (pressed), phyllaries strongly imbricate in 4(–5) series, inner (longest) 5–8 mm long, sparsely to densely evenly short-strigose to glabrate, eglandular; capitular bracts consistently present, ovate to elliptic-lanceolate, oblong-lanceolate, or narrowly lanceolate, ciliate with hairs 0.5–1.5(–2) mm long. **Ray flowers** 8–16(–20), corollas 9–12 mm. **Disc corollas** 4–6 mm. **Achenes** 2.5–3 mm, strongly flattened, with 3, raised, golden-resinous veins on each face, densely loosely villous-sericeous; outer pappus of narrow scales.

Flowering Jun–Sep(–Oct). Chaparral, pinyon-juniper, ponderosa pine (sometimes with aspen, oak, or ash), spruce-fir-aspen, rocky slopes, cliff bases, canyon walls, cracks and crevices, riparian habitats on cobble and sand or silty loam, roadsides; 3200–8300(–9200, –10,200) feet.

Collections of *Heterotheca fulciens* were annotated by Semple in 1993 as *H. fulcrata* vars. *fulcrata*, *amplifolia*, and *arizonica* and as variably mixed populations of vars. *fulcrata* and *amplifolia*. His maps of *H. fulcrata* (1996, Fig 28 A and B) appear to divide *H. fulciens* between his var. *fulcrata* and var. *amplifolia*, which are shown as sympatric in the range of *H. fulciens*. *Heterotheca fulciens* and typical *H. fulcrata* in the present treatment are allopatric.

1. With rhizomes or basal offsets; stems hirsute to villous-hirsute with variable length (not strongly 2-storied) hairs, eglandular or less commonly glandular; peduncles 2–4(–5) cm long; midcauline leaves 12–34 x 3–8(–10) mm, length/width ratio 2.8–7 /1 ..... 43. **Heterotheca fulciens**
1. Without rhizomes or basal offsets; stems with hirsute-villous overstory and puberulent, minutely glandular understory; peduncles (1–)3–8 cm long; midcauline leaves 15–55 x 5–17 mm, length/width ratio 2–2.8 /1 ..... 47. **Heterotheca fulcrata**

Nevada plants (Elko and Eureka cos.; e.g., Fig. 240) identified here as *Heterotheca fulciens* have prominent capitular bracts and are interpreted to be disjunct, western outliers of the species. In both counties, typical *H. cinerascens* is the only other goldenaster and is represented by abundant collections. Populational study is needed.

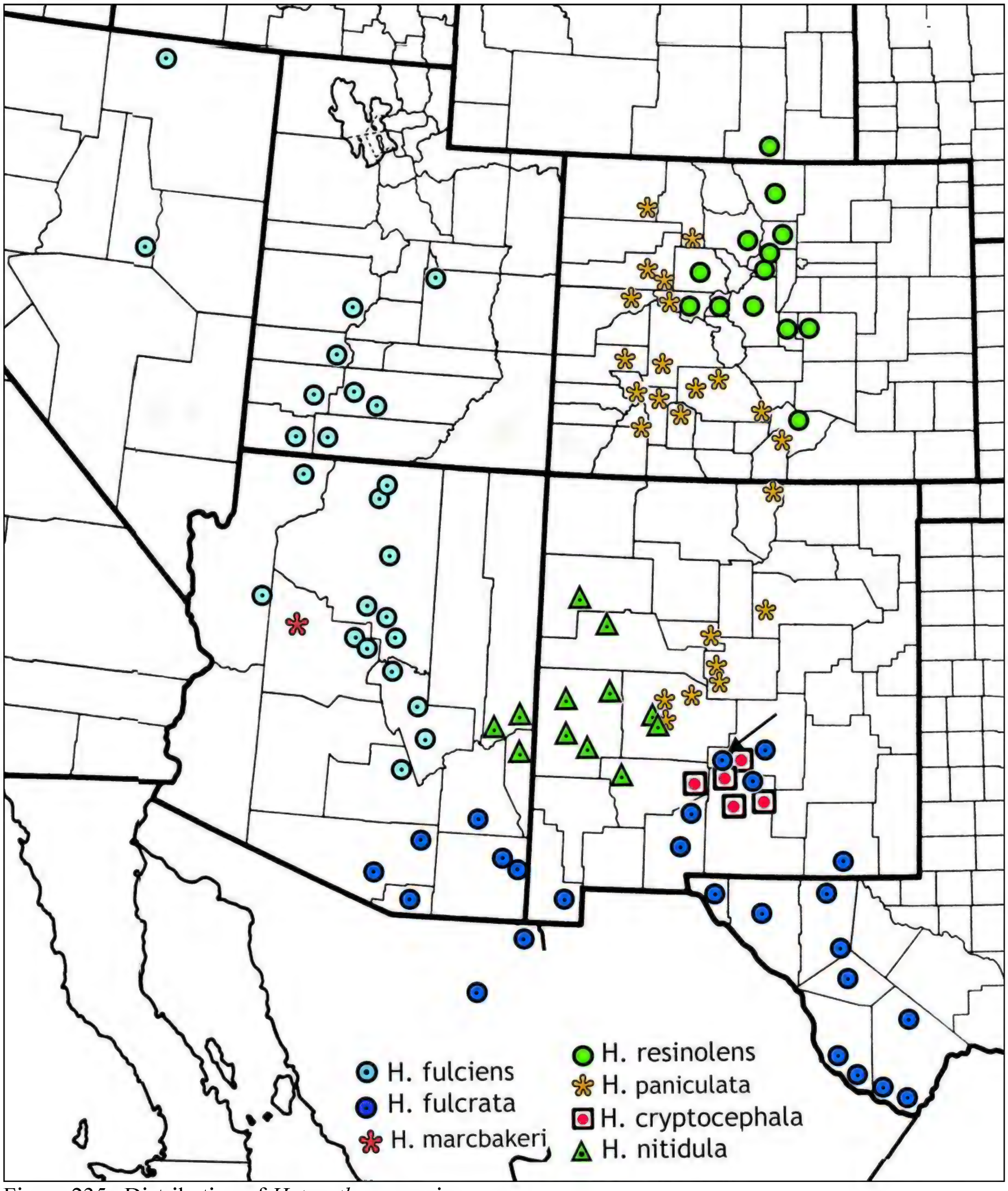


Figure 235. Distribution of *Heterotheca* species.

Figure 236. *Heterotheca fulciens*, holotype. *Coburn 1440* (ASU).

Figure 237. *Heterotheca fulciens*, Pinal Co., Arizona. *Baker 11261* (ASU).

Figure 238. *Heterotheca fulciens*, Yavapai Co., Arizona. *Licher 1337* (ASC).

Figure 239. *Heterotheca fulciens*, Coconino Co., Arizona. *Gilbert 181* (ASU).

Figure 240. *Heterotheca fulciens*, Eureka Co., Nevada. *Tiehm 11844* (RM).

A diploid chromosome number of $2n$=18 has been determined for *Heterotheca fulciens* from Coconino and Yavapai counties (*Semple 5546*, *7890*, 8999, 9005, 9007, *9009*, *9011*, *9013*; as noted on the labels). *Windham 96-267* from Coconino County vouchers a tetraploid chromosome count ($2n$=36) for a plant with unusually broad capitular bracts, perhaps suggesting that collections identified here as *H. fulciens* should be reexamined toward the possibility that two entities exist in sympatry (but ploidal variation exists within other species of *Heterotheca*). Capitular bracts of *Heterotheca fulciens* mostly are oblong-lanceolate to narrowly lanceolate but they vary to distinctly ovate.

Additional and representative collections examined. **Arizona.** Coconino Co.: 3.5 mi E of Jacobs Lake, 7600 ft, 27 Jul 1962, *Anderson 2148* (DS); Sycamore Canyon Wilderness, Cedar Creek, just S of Limestone Pocket, canyon bottom in ponderosa pine forest, 5840 ft, 5 Sep 1992, *Baker 10139* (OBI, RSA); Coconino National Forest, Clear Creek Wilderness Area, Forest Service Rd 81-E, USFS Trail #37 (Maxwell Trail), rim to stream bed with intermittent gravel beds, 6500 ft, 7 Jul 2003, *Bond 374a* and *Bond 398* (ASU); 2 mi N of Flagstaff, 7100 ft, 9 Sep 1961, *Breedlove 1202* (CAS); Grand Canyon, South Rim, Hull Cabin, Kaibab National Forest, 7100 ft, 9 Jul 1997, *Casey s.n.* (ASU); side of FS Road 610, ca 4 road mi NE Kaibab Lodge, spruce-fir-aspen, 9000 ft, 8 Sep 1993, *Christy 1936* (ASU); N Rim Grand Canyon, Swamp Lake Point, dry open hillside, 7522 ft, 14 Jul 1947, *Cooper 1901* (RSA); N Rim Grand Canyon, Powell Plateau, open woodland, 7555 ft, 14 Jul 1947, *Cooper 1913* (RSA); 7 mi S of Flagstaff, roadsides, 7000 ft, 24 Jun 1943, *Dearing 5489* (ASU); Pine Flat Hunting Camp, 6800 ft, 30 Aug 1945, *Darrow 2962* (CAS); near Jacobs Lake, 9 Sep 1938, *Eastwood & Howell 6411* (CAS); near Sunset Crater, 20 Sep 1938, *Eastwood & Howell 6964* (CAS); N rim of Grand Canyon, 21 Sep 1938, *Eastwood & Howell 7008* (CAS); 6 mi E of Jacobs Lake on Hwy 89, 27 Jul 1940, *Ferris 10242* (DS); 6 mi E of Jacobs Lake on US Hwy 89, ponderosa pine, N slope, 27 Jul 1940, *Ferris 10242* (RSA); W of FS Road 257, ridge E of Orderville Canyon, ca. 3 air mi NE of Jacob Lake turnoff on Hwy 89A, ponderosa pine, 7700 ft, 2 Aug 2003, *Fertig 20716* (BRY); Kaibab Plateau, E of FS Road 225C, ca 0.5 mi S of US Hwy Alt 89, ca 2 mi NE of Jacob Lake, ca 19 mi S of the Utah state line, E-dipping slope in small bowl in limestone bedrock on plateau within open ponderosa pine forest (understory recently burned), thin loam over limestone rubble, 2300 m, 26 Jul 2012, *Fertig 27680* (ASU); Coconino Natl Forest, mouth of West Fork Canyon of Oak Creek, about 9 mi N of Sedona, where WF joins Oak Creek, within northern section of Red Rock/Secret Mountain Wilderness, 1616 m, 29 Jul 2000, *Gilbert 181* (ASU); Grand Canyon, 1.5 mi N of Ranger Station, North Rim, rocky slope with southern exposure, 2500 m, 25 Jul 1964, *Halvorson 123* (ASU); Cape Royal Road, 4 mi N of Cape Royal, ponderosa forest, 2440 m, 8 Aug 1965, *Halvorson 205* (ASU); ca. 1 mi N of Bright Angel Point in seasonal housing area, aspen-ponderosa pine, 2540 m, 22 Aug 1965, *Halvorson 215* (ASU); Flagstaff, yellow pine, 700 ft, 23 Aug 1922, *Hanson 12* (MO); N Rim area of GCNP, 15 Aug 1965, *Harper s.n.* (BRY); San Francisco Peaks, N of Flagstaff, 8000 ft, 20-24 Sep 1945, *Heiser 1567* (MO, UC); ca. 4 mi S of Jacob Lake on Hwy 67, 8000 ft, sandy, ponderosa pine-aspen, 2 Aug 2001, *Higgins 28402* (BRY); 15 mi E of Jacobs Lake, yellow pine, 7000 ft, 8 Jul 1938, *Hitchcock et al. 4527* (CAS, WTU); near Shulz Pass Rd by golf course, ca. 7300 ft, 4 Sep 1976, *Hogue 316* (RSA); 3.5 mi from Flagstaff on Schultz Pass road, 7300 ft, 11 Sep 1968, *Howell & True 45068* (CAS); S of Grand Canyon, 6000 ft, 27 Aug 1923, *Jaeger 25* (POM); Flagstaff, 13 Aug 1884, *Jones s.n.* (POM); 28 mi past middle of Camp Verde on I-17N, ponderosa pine-gambel oak, ca. 6700 ft, 6 Sep 1990, *Keil 21420* (OBI); 1.5 mi SW of Jacob Lake, ponderosa forest, 6 Aug 1966, *Lehto 7011* (ASU); Walnut Canyon 7000 ft, 28 Jul 1898, *MacDougal 358* (NY-2 sheets, RM); Kaibab Forest, 5 Oct 1945, *Milner 8974a* (UC); Elden Mtn, 1 mi S 30° W of Little Elden Spring on E slope, 7550 ft, 27 Jul 1985, *Morefield & Roberts 2935* (RSA); off Old Munds Highway, near disc golf course in Pumphouse Wash, ponderosa pine forest, 2100 m, 7 Sep 2011, *Murray AZ932-90* (ASU); 22 mi N of Grand Canyon, 16 Aug 1974, *Nash N-264* (ASU), *Nash N-265* (TEX); road at Stoneman Lake, ponderosa pine zone, 2050 m, 16 Sep 1983, *Pinkava 14071* (ASU); Oak Creek, rocks, Oct 1903, *Purpus 8245* (UC); head of Oak Creek Canyon, 14 mi S of Flagstaff, beside hwy, 29 Sep 1959, *Russell, Smith, & Walters 10843* (ASU); Navajo Ordnance Depot, open places, 7200 ft, 13 Aug 1943, *Schallert s.n.* (CAS, MO, PH); 1 mi N of Parks, 7 Aug 1981, *Semple 5546* (ASU, BRIT, MO); US-89, 1.8 km E of Jacob Lake, open ponderosa pine woods, 7400 ft, 12 Sep 1985, *Semple 7890* (ASU, BRIT, MO); Schultz Pass Rd, off of US-180, N of Flagstaff, grassy ponderosa pine forest, locally

abundant, 2 Oct 1987, *Semple 9005* (BRIT, MO, ny, UC); 4 mi S of Flagstaff, US Hwy 89 along I-17, ponderosa pine, roadside of crushed lava, 3 Oct 1987, *Semple 9007* (MO); US Hwy 89, just S of Oak Canyon Viewpoint, steep rocky roadside embankment, 3 Oct 1987, *Semple 9009* (ASU, BRIT, MO); US-89, just S of Pine Flat Campground, Oak Creek Canyon area, oak, ash, and ponderosa pine, along roadside, 5500 ft, 3 Oct 1987, *Semple 9011* (ASU, BRIT, MO); US-89, S end of Coconino Natl Forest Recreation Area, Oak Creek Canyon, roadside, base of red sandstone cliffs, 4400 ft, 3 Oct 1987, *Semple 9013* (ASU, BRIT, UC); E of Flagstaff, Old Walnut Canyon Rd, ponderosa pine, 6800 ft, 28 Sep 1997, *White 5732* (RSA); W of Walnut Canyon Natl Mon., W Canyon Trail between trailhead and canyon escarpment, open ponderosa pine forest, 6750-6950 ft, 29 Sep 1997, *White 5760* (RSA); San Francisco Mts, Lockett Meadow, mesic grassy meadow, 8450-8550 ft, 10 Oct 1997, *White 5865* (RSA); San Francisco Mts, N side of mts, near "Lost Tank," dirt road ca. 1 air mi W of Hwy 89, open ponderosa pine forest, roadside, 1 Oct 1997, *White 5867* (RSA); NE of Sedona along Oak Creek near Grasshopper Point, ca 3.8 km SE of the summit of Wilson Mtn, sandy soil among alluvial boulders on N-facing slope, 4375 ft, 12 Sep 1996, *Windham 96-267*, **n = 18** (BRY, MO, NY). Gila Co.: Strawberry Hill, Mogollon Rim, N of Pine, ponderosa pine, 1800 m, 10 Sep 1970, *Collom 418* (ASU); Sierra Ancha Mts, Parker Creek drainage, Natural Drainage Expmtl Area, dry exposed ledges, 4700 ft, 25 Aug 1946, *Gould 3729* (SMU); Salt River Canyon, waterfalls area near Salt River Canyon Bridge, riparian, 27 Sep 1968, *Lehto 14243* (ASU); Sierra Ancha Mountains, Parker Creek Canyon, rocky canyon in chaparral area, 4000-4600 ft, 22 Jul 1968, *Pase & Keil 3399* (ASU). Mohave Co.: Mohon Mountains, upper Francis Creek near N boundary of Aquarius Planning Unit, along rock walls of canyon, chaparral-broadleaf riparian, 3900 ft, 14 Jun 1979, *Butterwick 5098a* (ASU). Pinal Co.: Dripping Spring Mountains; ca 6 km N of Hayden, E of Keystone Canyon, 200 m N of Chilito Mine, N face of low ridge, 3650 ft, 16 Nov 1993, *Baker 11261* (ASU). Yavapai Co.: NE of Prescott at Granite Creek, 0.6 mi E of jct Hwys 89/89A, granite outcrop, pinyon-oak, 5200 ft, 5 Sep 1991, *Atwood 17024* (BRY, RM, WS-possibly x *H. arizonica*); Sycamore Canyon Wilderness Area, Railroad Draw, 2 km N of Verde River, wash bottom, 4115 ft, 7 Oct 1992, *Baker 10324* (OBI); NW of Jerome, S of Little Black Mesa, 1.1 km SSW of Red Point Tank, Wildcat Draw, shallow limestone canyon, 1390 m, 25 Sep 1995, *Baker 11965* (ASU); R&S Ranch, West Clear Creek flood plain, N side of channel 1/2 mi E of confluence of West Clear Creek and Verde River, 975 m, 6 Oct 2006, *Bond 463* (ASU); 1.9 km S of Sycamore Canyon where it enters the Verde River, ca. 9 km N of Clarkdale, dry floodplain in cobble and sand, 1080 m, 10 Sep 2011, *Coburn 400* (ASU); Verde River at Perkinsville, ca. 200 m downstream from the bridge, shady, mesic riparian woodland, 1st terrace/ floodplain in silty-loam, 1170 m, 2 Oct 2012, *Coburn 1486* (ASU); Sycamore Creek; vicinity of Summers Spring, canyon bottom, 26 Jun 1992, *Govedich 62692-3* (ASU); Red Rock State Park, sandy flat above floodway, *Juniperus-Sapindus* woodland, 3880 ft, 23 Sep 2006, *Licher 1659* (BRY); Ariz Rte 179, SE of Sedona and ca 7 mi S of Coconino Co. line, pinyon-juniper zone, edge of Upper Sonoran Desert, 1136 m, 17 Sep 1983, *Pinkava 14083* (ASU); US Hwy 89 N of Prescott, crevices of large, locally abundant rock outcrops, 2 Oct 1987, *Semple 8999* (BRIT, MO). **Nevada**. Elko Co.: Bull Run Mts, slope due W of Bull Run Reservoir, limestone rock outcrops, 6000 ft, 16 Jul 1984, *Tiehm 9050* (BRY, CAS, ID! image!, NY, RSA, TEX). Eureka Co.: Fish Creek Range, Prospect Peak area SSW of Eureka, 1 road mi S of the peak, 8800 ft, with *Artemisia* on open gravel slopes, forming large clumps, 20 Jul 1988, *Tiehm 11844* (BRY, CAS, DES image!, ID! image, KANU image!, MO!, NY!, RM-Fig. 240, RSA, SRP image!, TEX!, UNLV, WTU). **Utah**. Beaver Co.: Tushar Mts, Beaver Canyon, oak-pinyon-juniper, rocky S-facing slope, 6400 ft, 29 Jun 1984, *Taye 2442* (UT). Emery Co.: NW of Huntington, Manti-La Sal Natl Forest, along State Rte 31, Bull Pasture Trail, narrow canyon with Huntington Creek on S side of hwy, N side an open slope with scattered Douglas fir, spruce, juniper, *Cercocarpus*, ca. 6000 ft, 21 Jul 2004, *Estes et al. 6616* (APSC). Garfield Co.: Escalante, sagebrush, 6700 ft, 8 Jun 1936, *Beck & Tanner s.n.* (BRY); Bryce Canyon Natl Park, Swamp Canyon bottom, sandy soil, 7340 ft, 17 Jul 1986, *Gottschalk s.n.* (UTC); between Torrey and Boulder near Hwy 12 summit, spruce-fir, 9200 ft, 20 Jun 1992, *Higgins 18885* (BRY); Hog Spring Ranch area, Dixie NF, ponderosa pine, igneous, bouldery soil, 8300 ft, 17 Jul 2006, *Madsen 3068* (BRY); Cons Hole at head of S Fork Oak Creek, Navajo sandstone, ponderosa pine-manzanita, 7700 ft, 12 Jun 2012, *Madsen 6007* (BRY); Paunsaugunt Plateau, Dixie Natl Forest, Johnson Ranch, ca. 7800 ft, 14 Jul 2014, *Madsen 6964* (OBI). Iron Co.: N side of Pine Valley Mts, vic. of Grant Ranch along Little Pinto Creek, 16 Jul 1973, *Atwood 5432* (BRY); Cedar Mtn, Ashdown Gorge Wilderness Area, ca 12.5 mi E of Cedar City,

terrace along perennial stream, spruce-fir, 7900 ft, 18 Aug 2009, *Fertig 25106* (BRY); Kolob Rd, 5 mi S of Cedar Canyon, open meadow with aspen, 8500 ft, 18 Aug 1977, *Foster 5335* (BRY). Kane Co.: Mt. Carmel, 14 Aug 1930, *Fuller s.n.* (MO); SC Vermilion, 4 mi N of Glendale, chippy shale, wet meadow community, 6600 ft, 17 Aug 1977, *Higgins 10922* (ASU, BRY, NY); top of the Pink Cliffs, ENE of the Straight Canyon trailhead, limber pine-ponderosa pine, 8700 ft, 23 Aug 2005, *Madsen 2650* (BRY, NY); 15 mi W of Orderville, left fork of Virgin River headwaters, yellow pine, 6600 ft, *Maguire 18858* (NY, WTU); Checkerboard Mesa, Navajo sandstone, 5 Jun 1984, *Neese et al. 15719* (BRY); E Fork Sevier River, spruce-fir, 8600 ft, 5 Aug 1976, *Welsh et al. 14317* (BRY). Millard Co.: Along Horseflat Canyon Creek, 5.8 mi SE of Kanosh and 1.8 mi S of Corn Creek Campground, just S of Second Creek, gravelly soil, open sagebrush slope and oakbrush community, 2000 m, 24 Jul 1991, *Atwood 15934* (ID-2 sheets); Canyon Mts, Eightmile Creek, 11.5 mi from Scipio, canyon bottom, 6800 ft, 13 Aug 1980, *Goodrich 14941* (BRY); Canyon Mts, Oak Creek near Oak Creek Campground and Guard Station, 4.2 mi SE of Oak City, quartzite outcrop with Gambel oak, 6300 ft, 7 Aug 1981, *Goodrich 16084* (ID-2 sheets, UT); Pavant Mts, Mine Camp Peak, aspens, 10,200 ft, 20 Sep 1980, *Greenwood s.n.* (BRY). Washington Co.: Zion Natl Park, West Rim between Potato Hollow and ranger cabin, telephone line trail, ca 7200 ft, 13 Jul 1949, *Bailey 3639* (UC); Zion Natl Park, Hidden Canyon Trail, 5 Jun 1940, *Braem 898* (DS); Zion Natl Park, E side of Spendlove Knoll, 25 Jun 1937, *Cockett 109* (UC); Pine Valley Mts, *Cercocarpus*-ponderosa pine, 8560 ft, 2 Aug 1968, *Gentry 2239* (WTU); Pine Valley Campground, sagebrush, 29 Aug 1937, *Gierisch 570* (WTU); Forest Camp, 3 mi E of Pine Valley, 7000 ft, *Artemisia tridentata* assoc. on dry slopes, 28 Jul 1942, *Gould 1950* (CAS, DS, NY, PH, UC) and 30 Aug 1942, *Gould 2066* (DS, NY, UC); Pine Creek, just N of Enterprise Reservoir, sagebrush-willow-rabbitbrush, 2000 m, 15 Aug 1985, *Higgins 16040* (BRY); Pine Valley Mts, Left Fork Santa Clara River, dry, rocky slope, 7200 ft, 13 Jul 1941, *Munz 16941* (POM, WS, WTU); Zion Natl. Park, Zion Canyon, 1-3 Aug 1925, *Pilbry s.n.* (PH); hillside above Kolob Canyon overlook, pine-juniper, 6500 ft, 16 Jun 1987, *Thorne 5348* (BRY, RSA); Zion Natl. Park, W Rim Trail, slickrock area above Refrigerator Canyon, sandy sites, 6000 ft, 7 Aug 1987, *Thorne & Chandler 5568* (BRY, NY, RM); ZNP, Church Mesa, 2.0 air mi E of Zion Lodge, S of Phantom Valley, near head of Coal Pits Wash, ponderosa pine, manzanita, 7250-7395 ft, 18 Jul 1988, *Thorne 6413* (BRY, RM); Pine Valley Mts, Pine Valley Recreation Area, riparian, 6800 ft, 22 Jul 1986, *Warrick 2601* (BRY, RM).

Variant (*Heterotheca fulciens* x *polothrix*?): **Arizona**. Coconino Co.: San Francisco Mts, 3 Nov 1880, *Greene s.n.* (POM). Stems and leaves hirsutulous and densely glandular; capitular bracts narrow; habit and aspect like *H. cinerascens*. Similar plants also are encountered in Washington Co., Utah.

44. HETEROTHECA MARCBAKERI Nesom, **sp. nov. TYPE: Arizona**. Yavapai Co.: [Apache Creek Wilderness Area], Apache Creek, 4.5 km W of Bald Mountain [Round Hill], N38 61 050 E3 26 250; T17N R6W NE1/4 NW1/4 section 9, granite boulders along creek, 5490 ft, with *Juniperus deppeana*, *Agave parryi*, *Juglans major*, *Rhamnus crocea*, *Arctostaphylos pungens*, *Cercocarpus montanus*, *Echinocereus coccineus*, *Opuntia engelmannii*, *Vitis arizonica*, *Artemisia ludoviciana*, *Eriogonum wrightii*, *Glandularia gooddingii*, *Hedeoma oblongifolia*, *Rosa woodsii*, and *Schoenocrambe linearifolia*; perennial herb with several dark green shoots rooted in cracks of boulders, 27 Aug 1992, *M.A. Baker 10080* (holotype: ASU; isotypes: OBI-2 sheets).

Distinctive in its woody taproot and short, scale-leaved basal offsets, congested and relatively even-sized, elliptic-oblong, sessile cauline leaves, lack of capitular bracts, minutely glandular stems and leaves, and evenly strigose, eglandular phyllaries. Different from *H. fulciens* in its apparently lack of elongate rhizomes, lack of capitular bracts, and eciliate phyllaries. Not similar to any other Arizona species. Known only from the type collection.

Figure 241. *Heterotheca marcbakeri*. Holotype (ASU).

Figure 242. *Heterotheca marcbakeri*. Isotype (OBI 53793).

Figure 243. *Heterotheca marcbakeri*. Isotype (OBI 50969).

Figure 244. *Heterotheca marcbakeri*. Left, isotype (OBI 53793). Right, holotype (ASU).

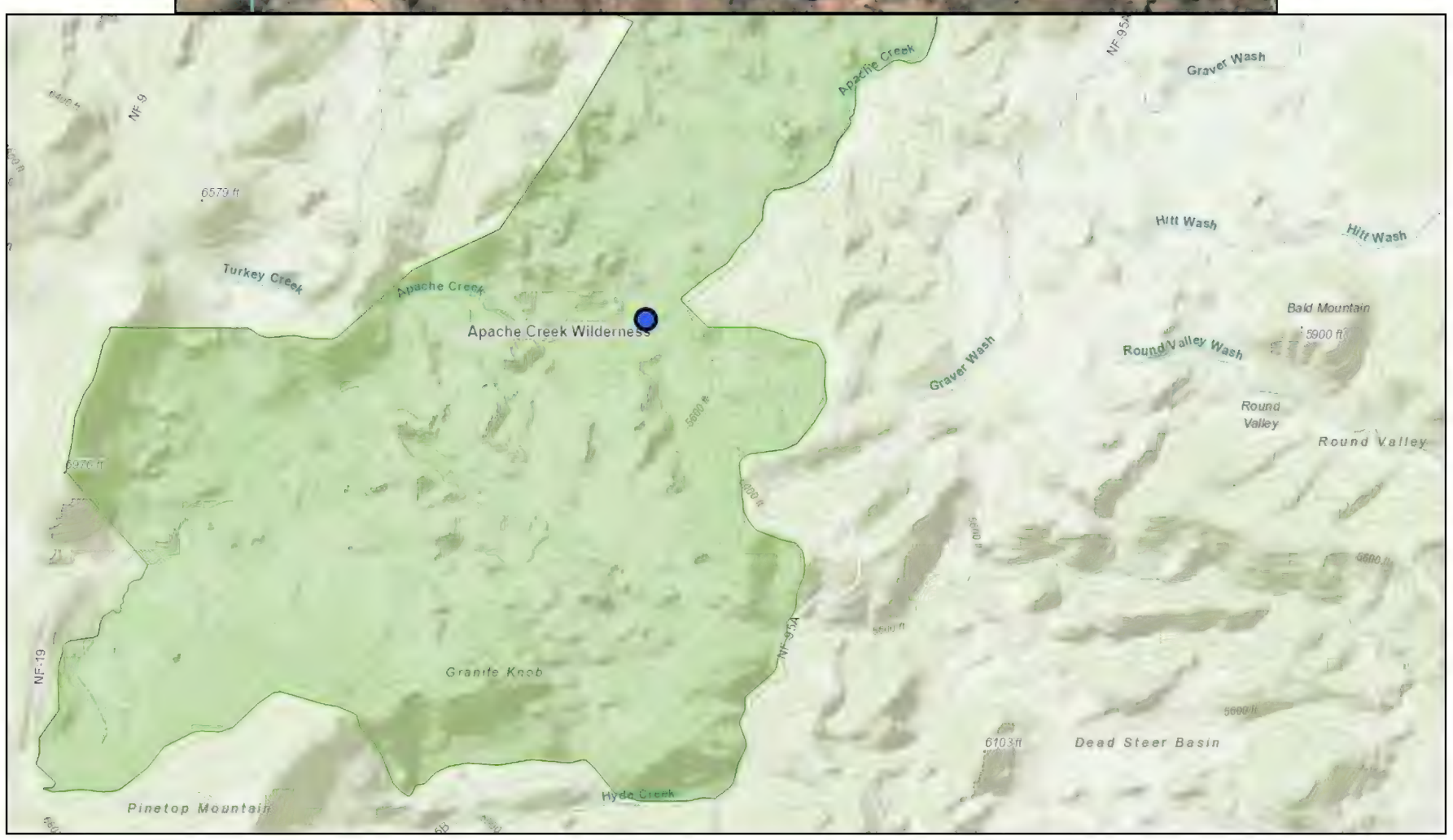


Figure 245. Distribution of *Heterotheca marcbakeri*. Above, location within Yavapai County, in the Santa Maria Mountains. Below, location along Apache Creek in the Apache Creek Wilderness, within Prescott National Forest. Bald Mountain, referred to in the label data, is at right-center. Google Earth and Google Maps.

Plants perennial from a woody taproot and short, scale-leaved basal offsets. **Stems** erect, 20–35 cm tall, unbranched or branched, hirsute, minutely glandular. **Leaves** elliptic to elliptic-oblong, elliptic-lanceolate, elliptic-oblanceolate, mostly 10–35(–40) mm long, sessile, base rounded to attenuate, cauline spreading to ascending, relatively even-sized or slightly decreasing distally, basal deciduous by flowering, surfaces hirsute to hirsute-strigose, minutely sessile-glandular. **Heads** mostly in short-pedunculate clusters, without immediately subtending capitular bracts; involucres 11–15 mm wide; phyllaries eciliate, with broad scarious margins, surfaces strigose, eglandular. Rays 18–24.

The new species probably is most closely related to *Heterotheca fulciens*, based on similarities in geography and morphology. Both produce rhizomes and/or basal offsets (offsets of *H. marcbakeri* are very short), leaves of similar shape and distribution, and relatively compact clusters of heads. Lack of capitular bracts is diagnostic of *H. marcbakeri*, and its heads are larger with more rays (involucres 11–15 mm wide, rays 18–24 vs. 6–9(–10) mm wide, 8–16 (–20)).

During study at ASU in 2015, I left the holotype sheet of *Heterotheca marcbakeri* unidentified because of its unsual morphology — the more recently encountered OBI duplicates indicate that the morphology is constant within the population and that the plants represent a distinct evolutionary entity.

The label for the type collection says "Woodchute Wilderness Area" but the other locality data, including geographic coordinates and township data, place it in the Apache Creek Wilderness (see Fig. 245) in the Santa Maria Mountains of northwestern Yavapai County. The only vascular plant collections from the Santa Maria Mountains (fide Seinet) apparently have been made by Marc Baker (in 1992 and 1998), and no other collections of *Heterotheca* have been made from there. The Apache Creek locality is at the edge of the range of *H. fulciens* — the collection of *H. fulciens* from the Mohon Mountains of southern Mohave Conty (*Butterwick 5098a*, ASU) is of typical morphology. Field work is necessary to see if the putative differences are consistent in a larger sample.

45. HETEROTHECA MARGINATA Semple, Rev. Heterotheca Phyllotheca, 83. 1996. **TYPE**: **Arizona**. Maricopa Co.: Superstition Mts., Apache Trail (AZ-88), 1.8 mi E of Tortilla Flats, 16 Oct 1993, *J.C. Semple 10384* (holotype: WAT; isotypes: ASU!, MO! image!, NY image!, UC!, US image!). Semple (1996) cited isotypes also at ARIZ, RM, and TEX.

Heterotheca marginata is morphologically distinctive and endemic to Gila, Maricopa, Pinal, and Yavapai counties and known from numerous collections. The species is characterized by relatively tall stems mostly erect from the base with hirsute, variably glandular vestiture, stiff, oblong-lanceolate leaves with densely hirsute surfaces, and long-ciliate margins of distal leaves and peduncular bracts (whence the epithet). Heads are on short, leafy-bracteate peduncles, compactly clustered distally and sometimes produced singly below on short, axillary, leafy-bracteate peduncles. Heads usually are subtended by short, linear to linear-lanceolate capitular bracts. Semple (1996) noted that both diploids and tetraploids occur within *H. marginata*.

Identifications and range delimitation here of *Heterotheca marginata* essentially agree with those of Semple. A collection from Gila County (S of Globe, *Semple 9029*, ASU) is identified by Semple as "aff. marginata" but I have identified it as *H. arizonica*. *Solomon 360* from Pinal County has unusually glandular leaf surfaces but it has coarsely ciliate margins and the aspect of *H. marginata*. Collections cited here from ARIZ were seen as images; all of those have been identified by Semple as *H. marginata*.

Additional collections examined. **Arizona**. Gila Co.: Along trail from 288 ca. 1 mi, 33.76, -110.97, 20 Oct 2007, *Farrugia 1561* (OBI); Pinal Mts, S of Globe, W side of Signal Peak off FS Rd 651, riparian, cutting through oak-pine, 6600 ft, 29 Jun 1980, *Forbes 1353* (NY); Sierra Ancha Mts, Parker Creek drainage, Natural Drainages Experimental Area, dry exposed ledges, 4700 ft, 25 Aug 1946, *Gould 3729* (LL, TEX, UC); Parker Creek Cañon, mtn mahogany, chaparral, 5400 ft, 17 Oct 1934, *Johnson J-30* (RM); Pinal Mts, 3.3 mi N of Pioneer Pass Rec. Area, chaparral-ponderosa pine transition, 24 Aug 1968, *Keil 3609* (OBI); Sierra Ancha, chaparral, 4500 ft, 8 Oct 1958, *Pase 1042* (RM); 21.4 km S of US 70, S of Globe, exposed road embankment, loose sandstone, 4 Oct 1987, *Semple & Chmielewski 9029* (MO). Maricopa Co.: Along road at Congress Junction, 24 Sep 1935, *Cutek & Christ 157* (MO); Fish Creek, Apache Trail, 29 Oct 1928, *Eastwood 15924* (CAS, LL, NY); 6 mi E of Tortilla Flat on Hwy 88, sandy soil, 2500 ft, 1 Oct 1986, *Landrum 5299* (ASU, NY); Tonto National Forest, ca. 3.3 mi W of Tortilla Flat near milepost 210 on Hwy 88 (Apache Trail), Canyon Lake, base of steep rocky N-facing slope, 1700 ft, 6 Oct 1997, *Landrum 9123* (ASU, NY); near Horse Mesa Dam, 2000 ft, 19 May 1935, *Peebles 11670* (ARIZ, LL); 3.2 mi on AZ-88, SW of bridge, E of Aracia, picnic site, 7.4 mi W of Tortilla Flats, 16 Oct 1993, *Semple 10383* (ASU, MO); Apache Trail (AZ-88), 1.8 mi E of Tortilla Flats, Superstition Mountains, 16 Oct 1993, *Semple 10384* (ASU); Apache Trail (Ariz Hwy 88) 2.8 mi E of Tortilla Flats, roadside, 16 Oct 1993, *Semple 10385* (UC); Apache Trail (AZ-88), 2.7 km E of Tortilla Flats, octotillo, desert 30 Sep 1995, *Semple 10499* (ASU). Pinal Co.: Devil's Canyon, 26 Sep 1926, *Fulton & Harrison 3102* (ARIZ); Apache Gap, Apache Trail, 2800 ft, 11 Oct 1931, *Gillespie 8540* (DS, UC); Superior-Miami hwy, upper tributaries of Queen Creek, 4500 ft, 23 Oct 1931, *Gillespie 8635.5* (DS, UC); above Superior, 12 Jun 1926, *Harrison 2093* (LL); Devil's Canyon near Superior, 12 Oct 1929, *Harrison & Kearney* 6309 (NY) and *6315* (ARIZ, LL); Martinez Canyon, NE of North Butte, north of Gila River, 23 Jun 1982, *Mittleman 14* (ARIZ); Devil's Canyon near Superior, 10 Oct 1926, *Peebles, Harrison, & Kearney 3192* (LL); Devil's Canyon, 4 Oct 1927, *Peebles & Harrison 4904* (ARIZ, LL); Tonto Natl Forest, Superstition Wilderness Area, Heiroglyphic Spring, 2 mi N of Hwy 60 at Gold Canyon Ranch turnoff, 2400 ft, 12 Oct 1991, *Rice 856* (OBI); Tonto National Forest, Superstition Wilderness Area, Miles Ranch trailhead, Forest Rd. 287, ca 12 mi from Hwy 60 to Red Rock Spring trailhead, oak-chaparral upland along perennial stream, 4400 ft, 20 Oct 1991, *Rice 890* (ASU); 3 mi E of jct US Hwy 80 and old Mesa Road, ca. 670 m, 17 Dec 1972, *Solomon 360* (MO). Yavapai Co.: along road from Prescott to Ash Fork, 18 Nov 1928, *Eastwood 16765a* (LL).

Figure 246. *Heterotheca marginata*, Maricopa Co., Arizona. Isotype (ASU).

Figure 247. *Heterotheca marginata*, Maricopa Co., Arizona. *Landrum 5299 (*ASU). Leaf and bract margins not as densely ciliate as in the isotype.

46. HETEROTHECA ARIZONICA (Semple) Nesom, J. Bot. Res. Inst. Texas 1: 27. 2007. *Heterotheca fulcrata* var. *arizonica* Semple, Brittonia 39: 380. 1987. **TYPE**: **Arizona**. Gila Co.: 0.3 km NW of East Verde River, Ariz. Hwy 87, NW of Payson, 13 Sep 1985, *J.C. Semple & S. Heard 7923* (holotype: NY digital image!; isotypes: ASU!, MO! digital image!, US, WAT).

Recognized by its consistently produced capitular bracts, small, basally attenuate, closely spaced leaves, the leaves and bracts with surfaces densely sessile-glandular and margins evenly ciliate wth short, thickened hairs. Stems, leaves, and bracts usually are distinctly green because of the reduced non-glandular vestiture.

Caespitose from a woody taproot; stems and leaves densely and prominently sessile-glandular to short stipitate-glandular, essentially green-colored because of the sparse, hirsutulous vestiture of nonglandular hairs. **Stems** ascending, (10–)15–40 cm high. **Leaves**: cauline elliptic to elliptic-oblanceolate or elliptic-lanceolate with an attenuate base, mostly 5–20 mm long and 1–5 mm wide, usually relatively even-sized, spreading or ascending, often with only the midvein visible and distinctly thickened and raised on abaxial surface, often with a thick-indurate, sharp-pointed, often recurving terminal mucro, margins evenly ciliate with short, thickened hairs. **Heads** solitary or on peduncles as short as 5 mm and distinctly clustered, usually immediately subtended by small, linear to narrowly oblanceolate capitular bracts, bract margins coarsely ciliate with thick-based hairs. **Involucres** 6–10 mm wide, 6–8 mm high; phyllaries glabrous to sparsely strigose, sometimes minutely sessile-glandular distally. **Ray flowers** 8–16(–20). **Chromosome numbers**, 2*n*=18 (*Semple 10498*, *Semple & Chmielewski 9028*, *Semple & Heard 8003*, *Semple & Heard 8004*), 2*n*=36 (*Semple & Chmielewski 9016*).

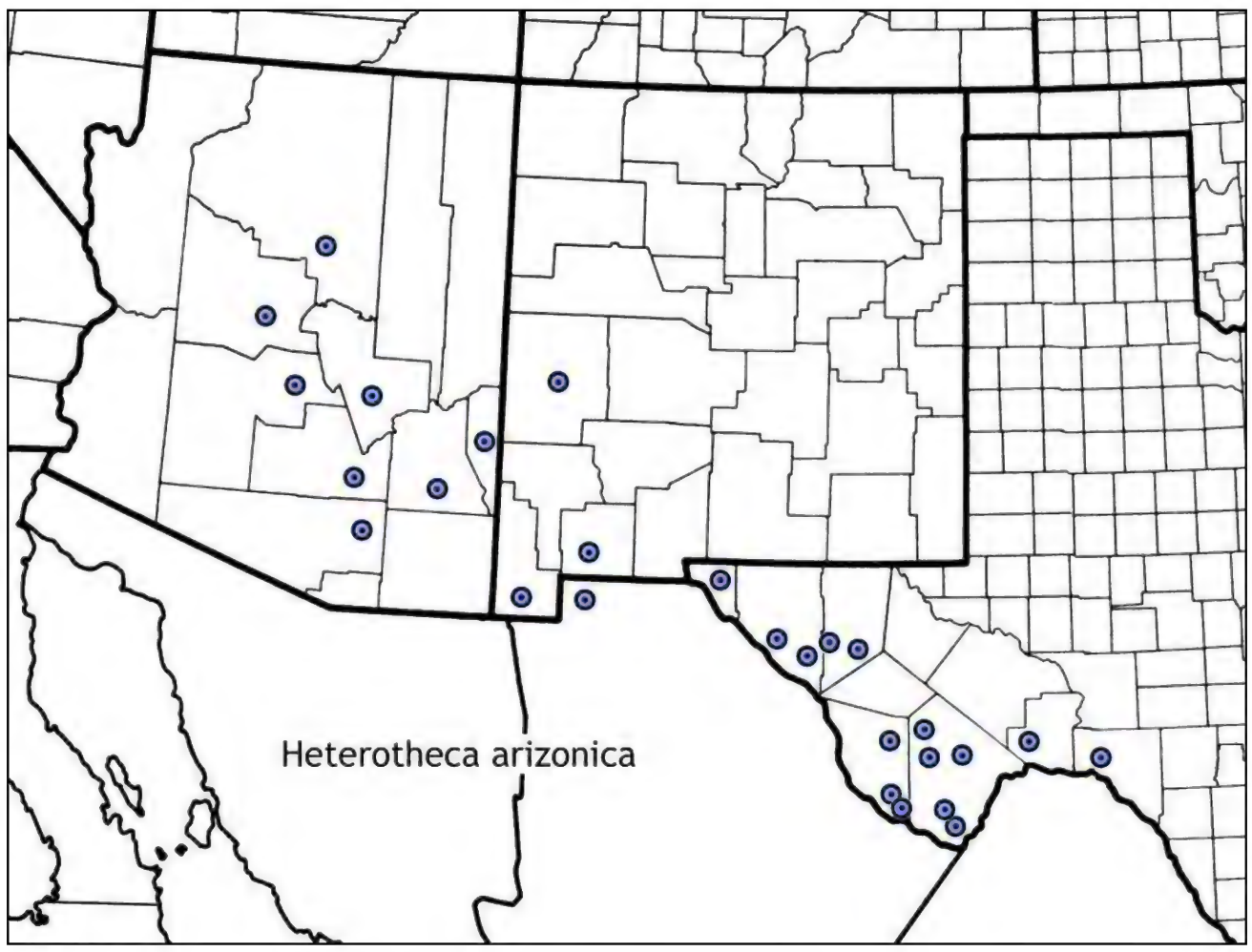


Figure 248. Distribution of *Heterotheca arizonica*.

In Arizona *Heterotheca arizonica* is sympatric with *H. fulciens* and with *H. marginata*. In the Chisos Mountains of Brewster Co., Texas, it apparently is uncommon — several collections show it growing there sympatrically with *H. chisosensis*: Young in 1915 collected both species at "Nail place," and *Warnock 1139* from the "wall of Casa Grande" has 3 branches of *H. chisosensis* and 3 of *H. arizonica* mounted on the same sheet. Other Chisos Mountains collections of *H. arizonica* were made by Mueller in 1931 and Warnock in 1941. It seems likely that *H. arizonica* grows in Mexico along the USA border.

Across the geographic range of *Heterotheca arizonica*, non-glandular stem vestiture is consistently spreading (slightly deflexed or up-flexed) to nearly absent, but in Culberson, Presidio, Terrell, Val Verde, and Brewster cos., Texas (e.g., in Brewster Co., *Cory 44980*, *Shinners 8693*, *Sundberg 1226*, and *Tharp s.n.* in 1931), it sometimes is antrorsely appressed. This perhaps reflects genetic influence of local variants of *H. fulcrata*, but (as noted above) typical *H. arizonica* and *H. fulcrata* growing sympatrically have been collected in the Chisos Mountains.

Representative collections examined. **MEXICO**. **Chihuahua**. Sierra de Moscos, *Chiang et al. 8711A* (TEX). **USA**. **Arizona**. Coconino Co.: Walnut Canyon, 16 Oct 1937, *Ramsey 2844* (POM). Gila Co.: Miami, granite rock mesa, 3 Sep 1937, *Gentry 3168* (CAS, RSA); Pinal Mountains, ca. 10.2 mi S of entrance to Tonto National Forest from Claypool on FR 55, then FR 651, ca. 2.6 mi N of Trail head 193, 2.3 mi W of trailhead 198, 6874 ft, 2 Nov 2003, *Gutierrez 439* (ASU); Sierra Ancha Wilderness Area, Tonto National Forest; on top of Aztec Peak E of lookout tower, *Pinus ponderosa*, *Quercus gambelii*, *Pseudotsuga menziesii*, 7700 ft, 6 Sep 1991, *Imdorf 132* (ASU); Tonto National Forest, ca 3 mi S of Pleasant Valley, 1/2 mi S of junction of FR 915 and FR 637, above Fourmile Canyon, open woodland, young granitic hills, 5621 ft, 1 Sep 2004, *Makings 1773* (ASU); Winkelman, desert with *Opuntia*, 27 May 1977, *Pinkava P-13817* (ASU); 7.0 km E of Superior on US Hwy 60, roadside and rocks, 30 Sep 1995, *Semple 10498* (MO); 4.1 km SW of Seneca on Hwy 60, red sandstone outcrop, 3 Oct 1987, *Semple & Chmielewski 9028*, 2*n*=18 (ASU, MO); Ariz Hwy 77, 21.4 km S of US-70, S of Globe, exposed road embankment, loose sandstone, 4 Oct 1987, *Semple 9029*, 2*n*=9II (ASU); US Hwy 60, rocks above Salt River, E of bridge, rocks and sandy soil just above river, 29 Sep 1995, *Semple 10497*, 2*n*=9II (ASU). Graham Co.: Pinaleno Mountains, Van Gausig Mountain, 1.5 mi W of AZ Hwy 6661, desert grassland on decomposed granite, 4700 ft, Jun 1976, *Bingham 2256* (ASU); Santa Teresa Mountains, BLM Wilderness, Jackson Mountain, E fork of Beauchamp Canyon, desert grassland, riparian, among rocks in narrow canyon, 4100 ft, decumbent perennial, 14 Aug 1998, *Buegge 487* (ASU); eastern foothills of Galiuro Mountains, ca 3.5 mi from end of High Springs Rd and on foot into hills, oak-pinyon pine-juniper woodland with grassy areas and patches of manzanita-dominated chaparral, on rocky slopes in full sun, 30 Sep 1989, *Keil 21263* (ASU). Greenlee Co.: Clifton, 1 Nov 1899, *Davidson s.n.* (RSA, UC); Clifton, 24 Oct 1940, *Goodding 85-40* (ASU); 2 mi N of Clifton, *Prosopis-Acacia-Senecio*, 6 Jun 1935, *Maguire 11821* (BRY, NY); Eagle Creek above confluence with Gila River, upstream from pump station, Vertical conglomerate canyon walls, 6 Sep 1998, *McGill 7007* (ASU); N of Clifton on US Hwy 666, S of Morenci, roadcut through alluvial deposits, 18 Sep 1985, *Semple & Heard 8003*, 2*n*=9II (ASU, MO); N of Clifton on US Hwy 666, 1 mi N of Morenci Rd, rock cuts and mine tailings, 18 Sep 1985, *Semple & Heard 8004*, 2*n*=9II (ASU, BRIT, MO, UC); S of Coronado Mountain, NW of Morenci, W of Coronado Gulch, ridgeline, 6830 ft, locally abundant perennial with dark green leaves, 13 Oct 1994, *Wright 1308* (ASU). Maricopa Co.: Apache Lake, rocky hills, 5 Oct 1938, *Gentry 3982* (RSA); Tonto National Forest, ca. 6.0 mi NE of Lost Dutchman State Park on Apache Trail at Canyon Lake Overlook, 1875 ft, 18 Jan 2004, *Gutierrez 504* (ASU); Four Peaks Wilderness, Cane Spring Canyon between Hidden Water Spring and Cottonwood Creek, permanent water, 1800 ft, 5 Apr 1989, *Jones 838* (ASU). Navajo Co.: grassland hike on roadside bluff, [W of Ariz Hwy 288 SW of Aztec Peak], 20 Oct 2007, *Farruggia 1601* (ASU). Pima Co.: Santa Catalina Mts, Redington Pass, 2 Oct 1939, *Benson 9753* (POM); Tortolita Mountains, Rail X Ranch Rd access, semi-desert grassland, 4018 ft, sprawling perennial, 11 Sep 2013, *Lindley 271* (ASU). Pinal Co.: Superstition Mts, S slopes, 18 Oct 1931, 4000 ft, *Gillespie 8614* (DS); Santa Catalina Mountains, Redington Pass, upper edge of the Lower Southern Desert, 4400 ft, 5 Oct 1938, *Glendenning 85* (ASU); Sierra Ancha, Aztec Peak, pine clearing, gravel, 7700 ft, 24 Aug 1958, *Johnson s.n.* (ASU); Tonto National Forest, Arnett Creek, turnoff about 4 mi S of Superior, riparian, seasonally dry, cottonwood-willow dominants, common in riparian-uplands transition among rocks, 2957 ft, 4 Oct 2005, *Makings 2235* (ASU); Oak Flats Recreation Area, near Globe, 3500 ft, 23 Oct 1952, *McCleary s.n.* (ASU); Superstition Wilderness Area, Tonto National Forest, Boulder Canyon trailhead, across from the Canyon Lake, *Juniperus deppeana*, *Pinus edulis*, *Platanus wrightii*, *Quercus emoryi*, common upland perennial, 5000 ft, 14 Sep 1991, *Rice 727* (ASU); US Hwy 60, 7.0 km E of Superior, roadsides and rocks, 30 Sep 1995, *Semple 10498*, 2*n*=9II (ASU); Pinal Mts near Craig Ranch, dry slope, 5200 ft, 14 Sep 1935, *Shreve 7464* (WTU). Yavapai Co.: 0.6 mi E of jct 89/89A, NE of Prescott at Granite Creek, granite outcrop, pine-

oak, 5200 ft, 5 Sep 1991, *Atwood 17024* (NY); road from Prescott to Ash Fork, 8 Nov 1928, *Eastwood 16765a* (CAS); Mescal Mts, 24 May 1890, *Jones s.n.* (POM); US Hwy 89, NE of Prescott, MP-317, crevices of large, locally abundant rock outcrops, 2 Oct 1987, *Semple 8999*, 2n=18 (ASU, NY). **New Mexico**. Catron Co.: SE edge of Plains of San Augustin, 14 mi SW of Horse Springs, vic. of Bat Cave, 16 Jul 1948, *Smith 87* (PH). Hidalgo Co.: E of Hachita, roadside, 14 Jun 1948, *Dittmer s.n.* (UNM digital image!); Little Hatchet Pass, 24 Aug 1970, *Turner & Powell 6092* (TEX, UC); Little Hatchet Mts, small limestone hills just W of Granite Pass, W end has igneous outcrops and cliffs, 4600-4800 ft, 18 Oct 1997, *Worthington 27328* (TEX, UNM digital image!). Luna Co.: Florida Mts, stream bed, 22 Jun 1957, *Jackson 2466-2* (UNM digital image!); Florida Mts, steep canyon on NW side of range, igneous, ca. 6000 ft, 12 May 1984, *Worthington 11932* (NMC, NY, TEX). **Texas**. Brewster Co.: Pena Blanca Mts [ca. 9 mi SE of Marathon], ca. 6 mi E of Hwy 385, in and around rock dikes in low mtns, 30 Sep 1962, *Correll 26104* (LL, SMU); S end of Del Norte Mts, limestone ridges, 6 Sep 1947, *Hinckley 4106* (NY); top of Elephant Mesa on Nevill Ranch, ca. 35 mi S of Alpine, dark volcanic rock, ca. 6100 ft, 20 Jun 1961, *Johnston 6424* (LL); 18 mi S of Alpine, hill near roadside park, 24 Aug 1976, *Kolle 1380* (TEX); Turtle Mtn., just W of the Corazones Peaks [70 mi S of Alpine, slightly NW of Big Bend NP], N of the Christmas Mts, 13 Aug 2017, *Ohl 122* (SRSC image!); 5 mi SW of Marathon, limestone slopes, 2 Aug 1946, *Shinners 8693* (SMU); 1 mi S of Terlingua, rock crevices, 21 Jul [no year], *Solbrig 3193*, **2*n* = 18** (NY); ca. 20 mi S of Marathon along Hwy 385, novaculite hillside, 17 Sep 2002, *Turner 22-239* (TEX); 3.3 mi S of Marathon along Hwy 385 from the Southern Pacific RR tracks, roadside cut in rocky chert (Caballo novaculite), 17 Jun 2003, *Turner 23-144* (TEX); wall of Casa Grande, 7000 ft, 15 Jun 1937, *Warnock 1139* (TEX–3 branches of *H. chisosensis* and 3 branches of *H. arizonica*); along Hwy 18 mi S of Alpine, frequent in igneous hills, 4300 ft, 26 Jul 1947, *Warnock 6616* (LL, SMU); [Chisos Mts, Big Bend Natl Park], Goat Mountain, 5 Aug 1941, *Warnock 20985* (BRIT); Chisos Mts, Nail place, dry slopes, 7 Aug 1915, *Young s.n.* (TEX). **El Paso Co.**: Hueco Tanks, rock crevices, 4000 ft, 17 Sep 1948, *Hinckley 4588* (NY); Hueco Tanks State Park, 15 Sep 1987, *Peterson 1147* (TEX); Hueco Tanks State Park, S end of boulders, 12 Jul 1976, *Powell 2996* (LL); Hueco Tanks State Park, 1 Nov 1973, *Riskind 1615* (BRIT, LL); Franklin Mts, McKelligan Canyon, 4 Nov 1942, *Shiner 40920* (TEX); vicinity of El Paso, 1941, *Stearns 154* (NY); SE side of North Mountain, 20 Aug 1977, *Van Devender s.n.* (TEX); near Hueco Tanks, cracks in granite cliffs, 20 Aug 1946, *Waterfall 6640* (NY) and *6640a* (NY); Franklin Mts, 0.5 mi SE of the top North Franklin Mountain, Ash Canyon Spring, 5700 ft, 20 Aug 1978, *Worthington 3194* — with large leaves, numerous heads, densely glandular stems and leaves, perhaps x *H. fulcrata* (TEX); Hueco Mts, Hueco Tanks State Park, N side of North Mtn, 4550 ft, 11 Aug 1979, *Worthington 4922* (BRIT). **Presidio** Co.: S side of Chinati Peak, crevices of igneous rock ledges, ca. 6900 ft, 7 Jun 1977, *Butterwick & Lott 3786* (TEX); Marfa, San Esteban Lake [10 mi S of Marfa], Jul 1936, *Hinckley s.n.* (TEX-2 sheets); just below San Esteban Lake, 12 mi S of Marfa, frequent on rocks, ca. 1300 m, Jul 1936, *Hinckley 698* (NY-2 sheets); Tierra Vieja Mts, near Vieja, clumps at edge of rimrock, 1950 m, 14 Aug 1941, *Hinckley 2085* (NY): upper Pinto Canyon on Watts ranch, 40 mi SW of Marfa, hanging from cliff crevices, ca. 5200 ft, 8 Jul 1942, *Hinckley 2538* (NY-2 sheets); head of canyon above Watts ranch house, on big boulders, 27 Aug 1943, *Hinckley 2846* (NY); Capito [Capote] Peak, 30 Aug 1944, *Hinckley 3245* (NY); branch of Cibolo Canyon (Chinati Mts], ca. 5 mi E of Russell Menzies ranch house, canyon walls, 4300 ft, 10 Aug 1947, *Hinckley 3971* (SMU); Big Bend Ranch State Park, Lower Monilla Canyon, 2690 ft, 13 Oct 2015, *Morey 297* (SRSC image!); top of Chinati Peak, common on bluffs, 21 Jul 1945, *Muller 8333* (LL, SMU). Terrell Co.: Route 41, 30 Aug 1946, *Albers 46172* (TEX); ca. 3 mi S of Sanderson, N-facing limestone bluffs, 13 Jun 1969, *Sikes 418* (TEX). Val Verde Co.: NW side of Pecos River, cliffs, 31 Oct 1966, *Correll 34054* (LL); Seminole Canyon State Historical Park, canyon rim overlooking confluence of Seminole and Presa Canyons, rock ledges and cliffs, 22 Nov 1987, *Labus 36* (TEX); ca. 7 mi ESE of Langtry, around edge of old RR tunnel near ruins of Vinagaroon, 7 Oct 1978, *Poole 1574* (LL, NY, VDB); Amistad Natl Rec. Area, Pecos River picnic area and boat launch, disturbed, gravelly (limestone) clay soils at base of massive, W-facing limestone roadcut, 24 May 2002, *Poole 4581* (TEX); Seminole Canyon State Park, limestone ledges and boulders above canyon, 8 Aug 1975, *Snyder 383* (SMU); Pecos River, 14 Jun 1931, *Tharp 8868* (TEX); Scenic Park overlook on Hwy 90, E bank of Pecos River, bare limestone bluffs, 14 Sep 1991, *M. Turner 2* (TEX); mouth of Pecos River, limestone soil in canyon tops, 1000 ft, 10 Aug 1967, *Warnock 22717* (TEX).

Figure 249. *Heterotheca arizonica*, Greenlee Co., Arizona. *Maguire 11821* (BRY).

Figure 250. *Heterotheca arizonica*, Brewster Co., Texas. *Warnock 6616* (LL).

Figure 251. *Heterotheca arizonica*, Gila Co., Arizona. *Jones 659* (ASU).

47. HETEROTHECA FULCRATA (Greene) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis fulcrata* Greene, Bull. Torrey Bot. Club 25: 19. 1898. **LECTOTYPE** (Shinners 1951): **New Mexico**. Lincoln Co.: White Mts., near Cherokee Bill's Spring, 6300 ft, 21 Aug 1897, *E.O. Wooton 511* (NDG 53811-Fig. 252; isolectotypes: AC, E, NY-2, P, US).

From among ND-G syntypes *Wooton 510*, *511*, and *512*, Shinners (1951) selected 511 as the lectotype. Harms (1968a, p. 17) entered a caveat: "This choice causes some confusion since Wooton and Standley (1913, 1915) obviously considered the first cited specimen, *Wooton 510* (NDG 53814-Fig. 253) from the Organ Mountains, as the true type of *C. fulcrata*, and their subsequent descriptions of *C. cryptocephala* and *C. senilis* seem based upon this understanding." *Wooton 512* was cited as a paratype in the protologue of *C. cryptocephala*, but there was never an explicit or formal statement by Wooton and Standley regarding lectotypification of *C. fulcrata*. Semple (1987) stated that "I consider all three Wooton syntype collections to be members of [*Heterotheca fulcrata*] var. *fulcrata* and accept Shinners' lectotype designation, *Wooton 511* (ND-G)." Semple's 1987 position is affirmed here and Shinners' choice appears to remain valid, notwithstanding Semple's later citation (1996, pp. 68, 70) and 1995 and 1997 annotations (e.g., NY, US) of 510 as lectotype.

Chrysopsis senilis Woot. & Standl., Contr. U.S. Natl. Herb. 16: 179. 1913. *Heterotheca fulcrata* (Greene) Shinners var. *senilis* (Woot. & Standl.) Semple, Brittonia 39: 380. 1987. **TYPE**: **USA**. **New Mexico**. Doña Ana Co.: Organ Mts., 4800 ft, 1 Sep 1897, *E.O. Wooton 509* (holotype: US image!; isotypes: MIN, MO!, NDG, NY image!).

Plants perennial, taprooted and caespitose from a thick, woody caudex. Stem vestiture 1- or 2-storied, hirsutulous to hirsute or hirsute-villous, less commonly loosely antrorsely strigose, eglandular. Leaves cauline (basal not persistent), oblong or obovate to oblanceolate or nearly spatulate, bases sessile (in blades with attenuate base) to truncate and subauriculate and sometimes subclasping, surfaces hirsute-villous to hirsute or hirsute-strigose, sparsely to densely sessile-glandular at least adaxially. **Heads** solitary or often on short branches in loose clusters of 2–5, peduncles mostly (1–)3–8 cm long, bracteate or ebracteate; capitular bracts 1–3(–4), oblanceolate to elliptic-oblanceolate or linear-oblanceolate, equaling or longer than the involucre. **Involucres** 8–10(–12) mm wide; phyllaries sparsely strigose at least distally to glabrate, sometimes densely strigose, eglandular. **Ray flowers** 12–18. **Chromosome number** 2*n*=18 (Culberson Co., Texas — *Semple & Heard 8170*, *Semple & Heard 8177*).

Flowering Jun–Sep. Open meadows and rocky ground, steep slopes, cliffs and cliff bases, talus, ledges and crevices, desert scrub, pinyon-juniper, pine-oak, ponderosa pine, pine-fir; 4200–8000 ft.

Heterotheca fulcrata in the strict sense is characterized by heads on leafy-bracteate peduncles, consistently with leaves and prominent capitular bracts densely long-ciliate (ciliate pustulate-based) at least along on the proximal margins. Semple's concept of the species included a broad morphological and geographical range of plants with capitular bracts. Segregates (presumably) from Semple's concept recognized here at specific rank include (at least in part) *H. arizonica*, *H. hirsuta*, *H. cryptocephala*, *H. fulciens*, *H. nitidula*, *H. paniculata*, and *H. resinolens* — the range of *H. cryptocephala* is at the northern margin of *H. fulcrata* sensu stricto in south-central New Mexico and mostly at higher elevations, while each of the others is allopatric with typical *H. fulcrata*.

Plants of *Heterotheca fulcrata* in the trans-Pecos Texas area, especially in the Chisos Mountains, tend to have antrorsely oriented, loosely strigose stem vestiture and oblanceolate leaves with sessile-attenuate bases, but the variation seems to be continuous with more typical morphology. In northern Coahuila, capitular bracts sometimes are reduced in size or formed slightly below the involucres and marginal cilia are relatively short.

Figure 252. *Heterotheca fulcrata*, Lincoln Co., New Mexico. Lectotype (*Wooton 511*, NDG).

Figure 253. *Heterotheca fulcrata*, Doña Ana Co., New Mexico. Paratype (*Wooton 510*, NDG).

Figure 254. *Heterotheca fulcrata*, northern Coahuila, Mexico, *Wynd & Mueller 593* (MO).

Additional (representative) collections examined. **MEXICO**. **Chihuahua**. Sierra de los Hechiceros, Cañón Encampanado, below (E of) Rancho Encampanado and above (W of) jct with Cañón de Indio Felipe, canyon bottom woods with perennial stream, on rock cliffs, 1300-1400 m, 27 Jul 1974, *Wendt & Adamcewicz 425* (LL, MEXU image). **Coahuila**. Mpio. Acuña-Ocampo, Sierra del Carmen, Rancho el Secadero, Cañon Poblano, 2100-2800 m, bosque de *Pinus cembroides*, *Quercus grisea*, *Crataegus greggiana*, *Juniperus flaccida*, *Ungnadia speciosa*, *Fraxinus berlandieri*, 20 Aug 1994, *Carranza 2082* (MO); Mpio. Ocampo, Sierra del Pino, Ejido Acebuches, Cañon La Vaca, bosque disperso de *Pinus arizonica* y *Juniperus flaccida* con *Arbutus xalapensis*, *Quercus intricata*, *Quercus gravesii*, *Quercus glaucoides*, 1850 m, 30 Sep 2005, *Carranza 3974* (MEXU image!); Sierra Jardin, ca. 8500 ft and above, 1 Sep 1966, *Flyr 1158* (SMU); SE of Big Bend Natl Park, S end of Sierra del Carmen, Canyon de Centinella, S side of Pico de Centinella, [date], *Henrickson 11659* (TEX); ca. 54 air mi SE of Big Bend Natl Park, S end of Sierra Maderas del Carmen, Cañon de la Fronteriza, 2 mi NE of Rancho San Isidro at end of Cañon del Alamo, rhyolite area, 1700-2000 m, 6 Aug 1976, *Henrickson 15033* (MEXU image, NY, RSA, TEX, UC); Sierra del Carmen, Canyon Hundido on N side of Pico de Centinela, E of Rancho El Jardin by winding road, steep canyon though igneous sierra, *Quercus* spp., *Pinus* spp., *Acer*, *Tilia*, *Garrya*, *Ceanothus*, *Fendlera*, *Pseudotsuga*, 1500-2250 m, 27 Jul 1973, *Johnston et al. 11818* (MEXU image, TEX); ca. 140 km NW of Muzquiz, Cuesta del Ploma area, ca. 3 road km S along road originating just SE of crest of Hwy 2A, high knob and long, sharply dipping ridge of soft 'rhyolite' atop limestone, juniper-oak-yucca on limestone, ca. 1640 m, uncommon, 4 Jun 1992, *Nesom & Mayfield 7432* (MEXU, TEX); Mpio. Ocampo, Maderas del Carmen Mts, [date], *Riskind et al. 1705* (TEX); Mpio. Villa Acuna, Serranias del Burro, Rancho El Bonito, Cañon El Toro, 18 Sep 1977, *Riskind 2158b* (TEX); Mpio. Ocampo, Sierra del Carmen, Cañon de la Fronteriza, 1520 m, 12 Aug 2004, *Riskind et al. 23880* (TEX); N slope of Pico de Centinelas, Sierra del Carmen, Canyon Hundido, 1900 m, 27 Jul 1973, *Riskind 11818* (NY not seen); Sierra del Carmen, 0.25 mi N of Campo Dos along trail to Campo Tres, along stream in moist canyon, mesic forest of *Pinus strobiformis*, *Pseudotsuga*, *Abies coahuilensis*, rhyolitic, 2325 m, common throughout the area, 7 Aug 1974, *Wendt & Adamcewicz 526* (LL, MEXU image); Mpio. Villa Acuña, Sierra del Carmen, Canyon de Sentenela on Hacienda Piedra Blanca, moist stream side, 8 Jul 1936, *Wynd & Mueller 593* (MO, TEX). **Sonora**. Base of San Luis Mts up to 6000 ft, 5 Sep 1893, *Mearns 2080* (CAS); Rio Bavispe region, Cañón Internacional, pine-oak, 23 Aug 1940, *White 3493* (ARIZ image!). **USA**. **Arizona**. Cochise Co.: Dos Cabezas Mts, Cooper Peak, upper oak woodland, 2130 m, 21 Aug 1976, *Bingham 2534* (ASU photo); Dos Cabezas Mts, Government Peak, NW-slope, granite, with mixed grasses, 11 July 1976, *Bingham 2654* (ASU photo); Bowie, 19 Sep 1884, *Jones 4296* (POM); Chiricahua Mts, Coronado Natl Forest, along Forest Rd 74, ca. 3 mi SE of Rucker Forest Camp, ca. 5800 ft, oak-juniper woodland, locally common on roadside, [small heads], 8 Aug 1992, *Keil 23762* (ASU, OBI); Bisbee, 28-30 Aug 1910, *Pilsbry s.n.* (PH). Graham Co.: Eastern foothills of the Galliuro Mts, ca. 3.5 mi from end of High Springs Rd and on foot into hills, oak-pine-juniper, [small heads], 30 Sep 1989, *Keil 21263* (OBI); 0.9 mi below Arcadia campground, oak hillside, 1460 m, 5 Nov 1967, *Lehto 10092* (ASU, OBI, UC); Pinaleno Mts, 0.8 mi above Arcadia campground, pine forest, 5 Nov 1967, *Lehto 10210* (ASU); Graham Mts, below Sawmill, 7-13 Sep 1914, *Thornber & Shreve 7784* (CAS). Maricopa Co.: Horse-dam Mesa [Superstition Mountains], 21 May 1929, *Eastwood 17379* (CAS). Pima Co.: Coyote Mts, Mendoza Canyon, along canyon bottom 1280 m, 17 Sep 1982, *Mittleman 461* (ASU); E slope of Rincon Mts, at highest point on Happy Valley road, under oaks, 4600 ft, 4 Sep 1946, *Pultz 1923* (CAS). Santa Cruz Co.: Santa Rita Mts, Baldy Trail, 7000 ft, 6 Nov 1924, *Bartram s.n.* (PH); Santa Rita Mts, Upper Josephine Canyon, stony slope, 7 Sep 1944, *Clark 12416* (RM); White House [Madera] Canyon, ca. 5100 ft, 2 Sep 1932, *Clausen 580* (DS); Santa Rita Mts, 4500 ft, 24 Aug 1903, *Jones s.n.* (POM); Santa Rita Mts, 7 Oct 1934, *Kearney & Peebles 10570* (DS); southern portion of Santa Rita Mts, 14.8 mi E from Amado along road to Mt. Hopkins (Whipple Observatory), woodland with riparian zone, roadside at canyon bank, pinyon-juniper-oak, 1930 m, 9 Sep 1985, *Keil 19025* (ASU, OBI); Santa Rita Mts, 10-20 Sep 1910, *Pilsbry s.n.* (PH); Madera Canyon, oak-pine woods, 1600 m, 21 Aug 1974, *Reeves R-1037* (ASU); Madera Canyon Trail, 1600 m, 13 Oct 1974, *Reeves R-1806* (ASU). **New Mexico**. Doña Ana Co.: San Andres Mts, Lower Goat Springs, 15 Aug 1950, *Fleetwood s.n.* (UNM digital image!). Eddy Co.: Carlsbad Caverns Natl Park, side canyon of West Slaughter Canyon, ca. 1.1 km S, 3.2 km W of jct of West and North Slaughter Canyons, limestone ledges, 22 Jul 1977, *Burgess 4639* (BRIT, TEX). Hidalgo Co.: Big

Hatchet Mtn Wilderness, Thompson Canyon, end of access road W into shady side canyon, desert scrub and rock-wall communities, 5870 ft, 13 Sep 2010, *Heil 32972* (SJNM). Lincoln Co.: Capitan Mts, along Forest Service Rd 56, doug fir-ponderosa pine-white fir, ca. 2300 m, 1 Aug 1976, *Wagner & Sabo 2176* (UNM). Otero Co.: SW of Ruidoso on US Hwy 70, 3.9 km N of Reservation Rd 4, SE-facing rocky road embankment and ditch, 21 Sep 1985, *Semple & Heard 8149* (BRIT). **Texas**. Brewster Co.: Rock crevices near summit of Mt. Emory, 7 Aug 1946, *Correll 13687* (SMU); Big Bend National Park, below Emory Peak, crevices of ledges, 17 Jun 1964, *Correll 29749* (LL); Window Trail, 7 Jul 1944, *Cory 44772* (TEX); North Wall, 10 Jul 1944, *Cory 44872* (LL); Iron Mountain [7 mi NW of Marathon, Gilliland Peak area], 13 Jul 1944, *Cory 44980* (TEX); Chisos Mts, Juniper Canyon, cliffs, 7400 ft, 15-18 Jul 1921, *Ferris & Duncan 2790* (NY); Chisos Mts., upper slopes of Green Gulch, 27 Aug 1944, *Lundell 13266* (LL, SMU); Chisos Mts, slopes of Emory Peak, crevices of rimrock, 2300 m, 22 Jun 1931, *Moore & Steyermark 3212* (NY, PH); Chisos Mts, 18 Jun 1931, *Mueller 8199* (NY); Boot Spring, 8 Jul 1932, *Muller s.n.* (SMU, TEX); Chisos Mts, 9 Jul 1932, *Mueller s.n.* (NY); Glass Mts, Old Blue, from base to summit on rocky limestone slopes, 18 Jun 1941, *Rose-Innes & Moon 1222* (TEX); Big Bend Natl Park, granitic cliff side near The Window, ca. 4500 ft, 4 Aug 1946, *Shinners 8743* (SMU); Big Bend Natl Park, The Basin, talus slope, ca. 5600 ft, 7 Aug 1946, *Shinners 8803* (SMU-2 sheets); 5 mi W of Alpine along Hwy 90, roadside, 16 Aug 1981, *Sundberg 1226* (TEX); Marathon, 15 Jun 1931, *Tharp s.n.* (TEX); 5 air mi W of Alpine, bluff along upper canyon, 28 Jun 1997, *Turner 97-229* (TEX); frequent on top of Pulliam Bluff, 2 Jun 1937, *Warnock 767* (TEX); wall of Casa Grande, 7000 ft, 15 Jun 1937, *Warnock 1139* (TEX–3 branches of *H. chisosensis* and 3 branches of *H. arizonica*); Glass Mts, Maple Canyon, infrequent in limestone crevices, 2 Aug 1940, *Warnock W275* (MO, TEX); W limestone slopes of Gilliland Peak, 5500 ft, 29 Aug 1947, *Warnock 6955* (SMU). N slope of Mt. Emory, igneous soil, 7500 ft, 10 Sep 1950, *Warnock 9706* (SMU); Glass Mts, W slopes of Old Blue Mountain on the Victor Pierce Ranch, limestone soil, 4700 ft, 27 Jun 1957, *Warnock & McBryde 15696* (LL). Culberson Co.: Guadalupe Mts, Pine Springs Canyon, 7 Sep 1961, *Correll & Johnston 24249* (LL); Hurd's Draw [or Herds Pass Draw, Jeff Davis into se Culberson Co.], buff silt (alluvial cover), hilly topography, 9 Jun 1949, *Janszen 40* (TEX); Guadalupe Mts, above Frijole, canyon near spring, 9 Aug 1945, *Lundell 14390* (LL, SMU); Guadalupe Mts, McKittrick Canyon, dry creek bed, 1890 m, 21 Jul 1931, *Moore & Steyermark 3529* (NY, PH); Guadalupe Mts, Smith Canyon (=Bear Canyon), 1.5-2 mi N of Pine Spring Canyon, rocky stream bed, 27 Nov 1963, *Oatman & Rowlett s.n* (TEX); Van Horn, sands, 10 Jun 1905, *Reverchon s.n.* (SMU); Guadalupe Natl Park, along Bear Canyon Trail, along creek, ca. 6400 ft, 23 Sep 1985, *Semple & Heard 8170* (BRIT); Guadalupe Natl Park, along Bear Canyon Trail, 7000 ft, 23 Sep 1985, *Semple & Heard 8174* (TEX); Guadalupe Natl Park, along Bear Canyon Trail at jct with Bowl Trails, ca. 8000 ft, 23 Sep 1985, *Semple & Heard 8177* (BRIT); Guadalupe Natl Park, along the Bowl Trail, very moist area at bottom of bowl, ca. 7700 ft, 23 Sep 1985, *Semple & Heard 8184* (BRIT); Guadalupe Mts, Smith Canyon, limestone crevices, 6200 ft, 10 Jul 1949, *Turner 1253* (SMU); Guadalupe Mountains, Smith Canyon, limestone soil, 5500 ft, 15 Sep 1948, *Warnock 121* (TEX); Guadalupe Mts, S of McKittrick Canyon, limestone soil, 5000 ft, 20 Jul 1954, *Warnock 11925* (LL); Guadalupe Mts, McKittrick Canyon, JC Hunter Ranch, limestone soil, 5 Sep 11954, *Warnock 12064* (LL, SMU); Guadalupe Mountains Natl Park, mid South McKittrick Canyon, 6500 ft, 25 Sep 1971, *Warnock 23365* (LL); Guadalupe Mts, Pine Spring Canyon, gravel bars above Pine Spring Camp, 23 Sep 1946, *Whitehouse 17090* (SMU); Chisos Mts, Nail place, the falls, 7 Aug 1915, *Young s.n.* (TEX). El Paso Co.: Southern Hueco Mts, along first drainage N of Four Mile Draw, ca. 30 mi E of El Paso, 25 Apr 1976, *Butterwick & Osborn 2593a* (BRIT); Franklin Mts State Park, Upper Fusselman Canyon, S of Loop 375, N of S Franklin Mountain, common on gravelly igneous and sedimentary slopes, 31 Oct 1989, *Carr 10225* (TEX); vicinity of Cottonwood Spring, W side of Franklin Mts, above Conutilla, crevices of rocks, 15 Oct 1952, *Correll 15054* (LL); Hueco Tanks, 32 air mi ENE of El Paso, granitic slopes, 12 Aug 1946, *Shinners 8933* (SMU); Franklin Mts, McKelligon Canyon, end of road, limestone gravel, 13 Aug 1946, *Shinners 8997* (SMU); Franklin Mts, mid McKelligon Canyon, limestone soil, 4200 ft, 31 Aug 1948, *Warnock 8241* (LL, SMU); Franklin Mountains, ca. 8 mi from El Paso toward the White Sands, limestone soil, E lower slope along the arroyos, 4600 ft, 28 Sep 1956, *Warnock 14230* (LL); El Paso, 24 Oct 1931, *Whitehouse s.n.* (TEX). Hudspeth Co.: NE end of Quitman Mts near Sierra Blanco, 4 Jul 1921, *Ferris & Duncan 2507* - densely glandular like *H. arizonica* (MO). Jeff Davis Co.: Cherry Canyon Ranch in N part of Davis Mts, E-W stretch of Eagle Waterhole Canyon, ca. 0.1-0.5 mi E of its mouth at Cherry Canyon,

Friend Mtn Quadrangle, local on unshaded rhyolite outcrops in open portions of pinyon-oak-juniper woodland on relatively mesic lowest portion of steep N-facing slope, 4760-4800 ft, *Carr et al. 23482* (TEX); Davis Mts, Madera Canyon, cliff crevices, 20 Aug 1946, *Correll 13997* (NY, SMU); Davis Mts, Fern Canyon, 15 Aug 1934, *Cory 9644* (LL); Davis Mts, Little Aguja Canyon, clefts of porphyritic cliffs, 12 Jun 1928, *Palmer 34530* (LL); Davis Mts, in the canyon of San Carlos Tunnel, among rocks on bluffs, rocky igneous soil, 22 Jul 1967, *Powell 1533* (TEX). Presidio Co.: Panther Canyon (Big Bend Ranch State Park), N of Hwy 170 and Rio Grande river, vicinity of Colorado Canyon, rocky streambed, 25 Jun 1975, *Butterwick B-1009* (TEX); W side of Chinati Mts, Scheele's Goat Ranch, crevices of syenite, 10 Sep 1961, *Correll & Johnston 24401* (LL, NY); Tierra Vieja Mts, below turn of ZH or Holland Canyon, walls and ledges of canyon, 1510 m, 20 Jun 1941, *Hinckley 1764* (NY); Cottonwood Canyon, ledges and cliffs just above first fall, 1510 m, 16 Jul 1941, *Hinckley 1966* (NY); Espy Miller ranch, ZH Canyon, rock crevices along creek, 11 Jun 1943, *Hinckley 2718* (NY); Sierra Vieja, Capote Canyon, ca. 1 mi below Capote Falls, 24 Jun 1973, *Sikes & Smith 658* (TEX).

A series of collections made by F.R Fosberg in 1930 from Doña Ana Co., New Mexico, includes some that appear to be intermediate between *Heterotheca fulcrata* and *H. zionensis*, both of which occur in the immediate area in typical morphology. The putative intermediates are similar in aspect to the Fosberg collections of typical *H. fulcrata* but marginal cilia are reduced in length and capitular bracts are absent; cauline leaves are silvery gray on crowded internodes, spreading in orientation, and with contorted margins; stems are hirsute-villous.

Typical *H. zionensis*: Doña Ana Co.: 2 mi NW of San Miguel, sand wash, 1200 m, 18 Aug, *Fosberg S3850* (POM, RSA).

Typical *H. fulcrata*: Doña Ana Co.: Canyon in S end of Organ Mts, base of cliff, 1580 m, 9 Oct, *Fosberg S3684* (RSA); mouth of canyon at S end of Organ Mts, porphyritic rocks, 1580 m, 9 Oct, *Fosberg S3713* (LL, RSA); Piño Blanca, S end Organ Mts, N slope, 1500 m, 11 Oct, *Fosberg S3950* (RSA).

Putative intermediates: Doña Ana Co.: Pyramid Peak, W slope, limestone ledges, 1380 m, 22 Jul, *Fosberg S3229* (RSA); 2 mi E of Vado, hills of andesitic porphyry, 1250 m, 4 Aug, *Fosberg S3347* (RSA); Pyramid Peak, W slope, limestone ledges, 1400 m, 12 Aug, *Fosberg S3736* (LL, RSA).

48. HETEROTHECA CRYPTOCEPHALA (Woot. & Standl.) Nesom, **comb. nov.** *Chrysopsis cryptocephala* Woot. & Standl., Contr. U.S . Natl. Herb. 16: 179. 1913. **TYPE**: **New Mexico**. [Lincoln Co.]: White Mts., V Pasture, Sect. 23, 23 Jul 1905, *E.O. Wooton s.n.* (holotype: US image!).

These plants are similar to *Heterotheca fulcrata* sensu stricto, but they occur only in a small region of south-central New Mexico. They produce prominent capitular bracts and oblong to elliptic, sessile, clasping to subclasping leaves, but leaves, stems, bracts, and phyllaries are sessile-glandular and only sparsely short-villous to hirsute-villous — because of much-reduced non-glandular vestiture, the whole plant has a distinctly green aspect. Capitular bracts 3–4(–5) per head, foliaceous and longer than the involucre, margins ciliate but usually not long-ciliate as in typical *H. fulcrata*. Involucres 9–12 mm wide. Ray flowers 10–18, corollas ca 15 mm long. The restricted geography is evidence that these plants are an coherent entity.

Flowering Jul–Sep. Grassy areas, cliff faces, roadsides and ditches, ponderosa pine, ponderosa pine-oak oak-ash; 6800–9000 ft.

Additional collections examined. **New Mexico**. Lincoln Co.: White Mts, N edge of Ruidoso, road to Montgomery Field Station, S-facing roadcut, doug fir, ponderosa pine, and Gambels oak, 6900 ft, *Ward & Spellenberg 81-449* (NY). Otero Co.: Sacramento Mts, La Luz Canyon Road, ca. 1/2 mi W of Apache Canyon, ponderosa pine-oak, 7320 ft, 26 Jul 2001, *Allred 8121* (BRY); western slopes of the Sacramento Mts, Lincoln Natl Forest, La Luz Canyon, Apache Canyon (small side canyon), grassy open area in mixed conifer forest with ponderosa pine, sw white pine, 7720 ft, 23 Aug 2002, *Allred 8341*

Figure 255. *Heterotheca cryptocephala*, Otero Co., New Mexico. *Baker 14698* (ASU).

Figure 256. *Heterotheca cryptocephala*, Otero Co., New Mexico. *Baker 14698* (ASU), same collection as in Fig. 255, showing consistency of morphology within the population.

(NMCR); Sacramento Mts, 7 km SW of Sacramento, above Hoosier Canyon, limestone cliff and associated talus within burned and mostly killed *Pseudotsuga menziesii-Pinus ponderosa-Abies concolor* forest, 2530 m, 17 Aug 2002, *Baker 14698* (ASU-2 sheets, BRIT); SW of Ruidoso on US-70, 3.9 km N of Reservation Rd #4, rocky road embankment and ditch, 21 Sep 1985, *Semple & Heard 8149* (MO, NMC, UC); White Mts, 6200 ft, 19 Aug 1897, *Wooton s.n.* (RM). Sierra Co.: White Sands Missile Range, Salinas Peak, alongside building (S side) on top, 8965 ft, 10 Aug 1996, *Anderson 6859* (TEX).

49. HETEROTHECA NITIDULA (Woot. & Standl.) Nesom, J. Bot. Res. Inst. Texas 1: 24. 2007. *Chrysopsis nitidula* Woot. & Standl., Contr. U.S. Natl. Herb. 16: 179. 1913. **TYPE**: **New Mexico**. [Catron Co.]: Mogollon Mts., on or near the West Fork of the Gila River, 7500 ft, 20 Aug 1903, *O.B. Metcalfe 552* (holotype: US, Fig. 257; isotypes: AC image!, GH image!, MIN image!, MO!, NMC!, RM! image!).

The description and labels say "Socorro Co." but redefined county boundaries now place the type locality in Catron County.

Heterotheca nitidula is endemic to west-central New Mexico and the White Mountains of adjacent Apache and Greenlee counties, Arizona. It is similar to *H. fulcrata* in its prominent capitular bracts but distinctive in its relatively narrow and more elongate leaves (mostly narrowly oblanceolate, 3–5.5 cm long, 3–8 mm wide, attenuate to the base), relatively long rays (10–12 mm long), and particularly in its strigillose vestiture. *Heterotheca nitidula* (like *H. fulciens*) produces basal offsets and short rhizomes and is distinctive in habit from typical *H. fulcrata*. Heads solitary or usually in clusters of 2–6 and usually (sometimes variable on a single plant), immediately subtended by lanceolate capitular bracts. Stems, leaves, bracts, and phyllaries minutely glandular and sparsely to moderately strigillose with a nonglandular vestiture of extremely thin, slightly flexuous, closely appressed hairs 0.5–1.5 mm long, without enlarged basal cells (use 10x lens to see clearly).

Plants of *Heterotheca nitidula* in the Zuni Mountains area of Cibola and McKinley counties appear to be set apart geographically and have a reduced amount of nonglandular vestiture and often a slightly glaucous aspect (e.g., Fig. 260).

Flowering Aug–Sep(–Oct). Open rocky slopes and flats, ridges, ledges dry grassland roadsides, meadows, pinyon-juniper, limber pine, ponderosa pine, ponderosa pine-mixed conifer, spruce-fir, spruce, (7000–)7400–10,400 feet. $2n$=18 (*Semple & Heard 8021*; *Turner 5700*).

Additional collections examined: **Arizona**. Apache Co.: Apache Natl Forest, Mount Baldy area, W Fork Little Colorado River, parking area off State Rd 273, locally abundant in dry grassland, 2787 m, 21 Sep 1998, *Brant & Stone 4128* (MO, TEX); Greer, Riverside Ranger Station, 2700 m, 24 Aug 1920, *Eggleston 17157* (NY); White Mts, Black River, Thompson's Ranch, 14 Jul 1910, *Goodding 602* (RSA); White Mts, Thompson's Ranch, steep W slopes, 14 Jul 1910, *Goodding 602* (NY); Alpine, open flats, 31 Jul 1912, *Goodding 1259* (CAS, NY, WTU); White Mts, 6-15 Aug 1903, *Griffiths 5329* (MO); along Forest Rd 275 in Stone Creek drainage, above stream in gravelly soil, 8000 ft, 11 Aug 1998, *Hammond 11478* (TEX); White Mts, dry road shoulders, 8500 ft, 15 Aug 1973, *Moldenke 27846* (LL); Apache Natl Forest, along Nutrioso Creek and US Hwy 180/191-Coronado Trail, ca. 5.5 air mi NNW of Alpine, meadow above the creek, 8080-8120 ft, 21 Sep 2005, *Nelson 67212* (RM); Apache Natl Forest, White Mts, along Benny Creek, ca 1 air mi W of S end of Greer, meadow, 9050-9140 ft, 3 Sep 2006, *Nelson 70834* (RM); Apache Natl Forest, Greens Peak, ca 16.5 air mi W of Springerville, electronic site on rocky, open mtn top, 10,000-10,133 ft, 4 Sep 2006, *Nelson 70967* (RM); 8 mi E of Nutrioso, ridge above Milk Canyon Escudilla Mtn, 8500 ft, yellow pine assoc., 24 Aug 1951, *Parker & McClintock 7545* (CAS); near Greer, 8300 ft, 19 Aug 1935, *Peebles 12555* (LL); Sheep Crossing Campground [Hwy 273 near Greer], spruce-fir, 9200 ft, *Pinkava, Brown, and McLeod 503*, 20 Aug 1971 (ASU); E edge of Alpine on US 180, road embankment, red shale, limber pine, 8030 ft, 19 Sep 1985, *Semple & Heard 8021*, **2n=18** (ASU, BRIT, NY); N of Greer, Rte 373 near Rosey Creek Rd, 22 Aug 1973, *Sexton s.n.* (ASU); 12 mi N of Alpine, common in roadside cuts, 13 Aug 1967, *Turner 5700*, **2n=18** (TEX); Sitgreaves Natl. Forest, 5.4

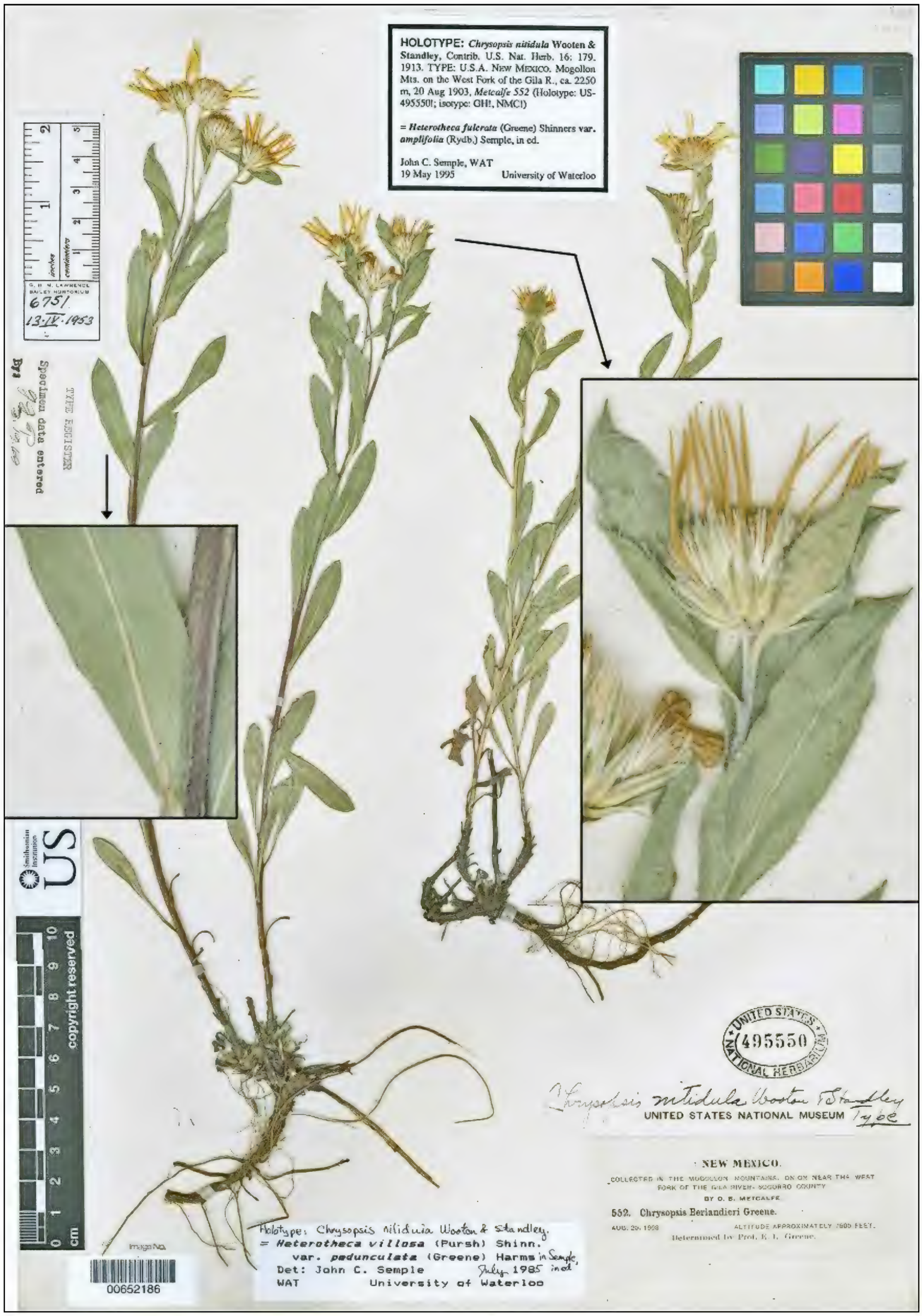


Figure 257. *Heterotheca nitidula*, holotype. Catron Co., New Mexico.

Figure 258. *Heterotheca nitidula*, Cibola Co., New Mexico. *Riffle 804* (UNM).

Figure 259. *Heterotheca nitidula*, Socorro Co., New Mexico. *Hutchins 4758* (UNM).

Figure 260. *Heterotheca nitidula*, McKinley Co., New Mexico. *McCallum 1378* (UNM).

mi S of jct US 666 and US 180 on 666, E of road in meadow, 15 Aug 1978, *Warnock 1677* (TEX). Greenlee Co.: Apache Natl. Forest, 10 mi E of Big Lake on Forest Rd 249 and 8 mi from Alpine, near turnoff to Sierra Blanca and on hillside above lake in rocky soil, open areas in spruce forest, 8900 ft, 16 Aug 1972, *Hess 2937* (SMU). **New Mexico**. Catron Co.: ca. 10 mi E of Beaverhead in open yellow pine forest, ca. 8000 ft, 28 Sep 1951, *Dunn 7716* (RSA); Datil Forest, Sec 33 T10S R14W, 10 Sep 1926, *Ewing 6* (RM); Mogollon Mts, Gila Natl. Forest, Indian Creek drainage and Bear Wallow Mtn, common perennial on E-facing slope and drier areas, 9200 ft, 4 Sep 1968, *Hess 2394* (NMC, SMU); Gallo Mts Jewett Gap, milepost 18, 8160 ft, 27 Aug 1997, *Hubbard s.n.* (UNM image!); Mogollon Mts, 1.4 road mi N of Gilita Campground, ponderosa pine, ca. 8100 ft, 7 Sep 1978, *Moir & Fitzhugh s.n.* (NMC); Mogollon Mts, 7 Sep 1881, *Rusby 167* (UC); Mogollon Mts, high rocky summits, 7 Sep 1881, *Rusby 168* (MO, NY-3 sheets; PH); 3.3 km W of Luna on US 180, 5.5 mi E of NM state line, open ponderosa pine, 19 Sep 1985, *Semple & Heard 8027* (UC); Mogollon Mts, Forest Rd 141 just N of Negrito Work Center, open parkland, ponderosa pine, 12 Aug 2008, *Sivinski & Lowrey 6930* (UNM image!); Gila Natl Forest, 13 mi straightline NNE of Beaverhead Ranger Station, near NM 163 and FS 150, montane grassland and pinon-juniper woodland, SW-facing slope, sandy, rocky ash flow, 7500 ft, 3 Oct 1995, *Williams 2600* (NMC). Cibola Co.: Zuni Mts, jct of Forest Service Rd 3178.1 and 3180, ponderosa pine area, 7800 ft, 17 Aug 1968, *Riffle 783* (UNM image!); Zuni Mts, SE slope of Mt Sedgwick, rock ledges close to the summit, 9200 ft, 17 Aug 1968, *Riffle 804* (UNM, Fig. 258); Zuni Mts, road jct at base of Mt Sedgwick, 8900 ft, 21 Sep 1968, *Riffle 1068* (UNM image!). Grant Co.: Mogollon Mts, on or near the West Fork of the Gila River, ca. 7500 ft, 20 Aug 1903, *Metcalfe 552* (NY, UC). McKinley Co.: Zuni Mts, McGaffey Camp off NM Hwy 400, open fields, 2800 m, 30 Jul 1964, *Baad 1075* (WTU); Cibola Natl Forest, [Zuni Mts], Cottonwood Canyon, abundant on open slope, 28 Aug 1981, *McCallum 1378* (UNM-2 sheets, Fig. 260). Sierra Co.: Black Range, Stiver Spring area [Taylor Peak area], gravel and sandy loam of ponderosa pine-mixed conifer area, 7900 ft, 13 Aug 1982, *Hutchins 10374* (UNM image!); Black Range, Diamond Creek, S-facing slope, 12 Aug 1982, *Knight 2282* (UNM image!); Taylor Creek, ca. 14 air mi E of Beaverhead, rocky S-facing slope with ponderosa pine, 7400 ft, 14 Aug 1982, *Spellenberg et al. 6598* (NMC). Socorro Co.: Socorro [Magdalena Mts], rocky fertile open wooded hillside, 8000 ft, 18 Aug 1968, *Demaree 59017* (COLO image!, RSA, UNM image!); San Mateo Mts, Cibola Natl Forest, FS Rd 138, ca. 6.0 mi N of FS Rd 330, 9735 ft, 15 Aug 2009, *Heil 31540* (SJNM); Magdalena Mts, South Baldy, SE slope, gravel loam, ca. 10,400 ft, 26 Aug 1973, *Hutchins 4758* (UNM, Fig. 259); Magdalena Mts, vicinity of Water Canyon, gravel loam, 9800 ft, 30 Sep 1973, *Hutchins 4889* (UNM image!); Magdalena Mts, vicinity of Water Canyon, gravel loam, 10,300 ft, 13 Jul 1974, *Hutchins 5053* (UNM image!); Magdalena Mts, N side of Timber Peak, head of Water Canyon, 8300 ft, 11 Sep 1959, *Martin 3684* (UNM image!); Middle Fork of Gila, 7500 ft, 5 Aug 1900, *Wooton s.n.* (NMC).

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TYPIFICATION OF *SOLIDAGO RETRORSA* MICHX. (ASTERACEAE: ASTEREAE)

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ABSTRACT

Solidago retrorsa was published by André Michaux in 1803 and placed in synonymy under *S. odora* by Asa Gray (undated annotation). The Michaux herbarium includes five sheets that are likely original material on which typification of the name can be based. One of these collections is selected as the lectotype and two other collections are considered to be possible isolectotypes or syntypes; all are identified as *S. odora*. The fourth and fifth collections treated as *S. odora* are identified as *S. tortifolia*, an unrelated species.

As part of the work being done by the first author to complete a monograph of the entire genus *Solidago* L., numerous small nomenclatural problems have to be resolved. One of these is the identification of possible type material for the name *Solidago retrorsa* Michx. (Fl. Bor. Amer. 2: 117. 1803). With the help of the staff of the Muséum National d'Histoire Naturelle in Paris in locating, identifying, and annotating possible type material for *S. retrorsa*, three collections were found among specimens in the André Michaux collection (P-MICH) and in the general collection that had been labeled as *S. retrorsa* at some point in the past, although none were annotated as type specimens. Each collection is discussed below. Two additional collections were labeled as *S. odora* Ait.

The first herbarium sheet from the André Michaux collection has a label in Michaux's handscript with the following information "Solidago retrorsa" at the top of the label and "Basse Caroline" "Bois pres l'habitat" [wood near populated area, transl. FJ) on the bottom of the label. The specimen consists of an upper stem with some leaves and a large apically secund conical inflorescence with flowering and fruiting heads. This collection has been identified by the first author as *S. odor*a Ait. (Fig. 1).

A second herbarium sheet has two smaller shoots on the sheet and several labels (Fig. 2). The label in the lower left corner of the sheet has in a different handscript from the first collection "Solidago retrorsa," "Ameriq: Sept." and "Michaux" in ink and "S. odora A.G." in pencil in Asa Gray's distinctive script. The label on the lower right corner is a Mus. Nat. Paris label with "Solidago odora A. (ex Asa Gray!) S. retrorsa Michx." written in ink in Edouard Spach's handscript. The two shoots are possibly Michaux collections made at the same time as the first collection or at a different time on the same expedition from a different location; there are insufficient data to know for certain. Both shoots on this second herbarium specimen have been identified as *S. odora* by the first author.

Figure 1. Lectotype of *Solidago retrorsa* Michx. *Michaux s.n.* (P-MICHX). Barcode: P00320362. <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320362>

Figure 2. Possible isolectotype/syntype of *Solidago retrorsa* Michx. *Michaux s.n.*, on left (P). Barcode: P02512809. <http://coldb.mnhn.fr/catalognumber/mnhn/p/p02512809>

A third herbarium sheet in P (Fig. 3) has two mid to upper stem shoots with inflorescences and a label with "Solidago retrorsa." and "Michaux" in black ink and "Herbarium Richard" in red ink at the top. The largest mid stem leaf is entire and has a prominent midvein. The inflorescences have long lower branches and bear heads that range from immature to fruiting. The first author identified these shoots as *S. odora*.

A fourth herbarium sheet, stored in the André Michaux collection, consists of four upper shoots (Fig. 4) and bears a label with André Michaux's handscript "Solidago odora Ait./ Virga aurea americana/ Tarraconis facie et sapore, --- panicula copiosisima/ Pluck Phytogr T.116.f.6." These shoots are all identified by the first author as *Solidago tortifolia* Ell., having leaf shape and small leaf margin serrations typical of that species, and the larger leaves are triple-nerved as found in *Solidago* subsect. *Triplinerviae* (Torr. & A. Gray) Nesom and not like *S. odora* which has entire single-veined leaves without serrations (Semple & Cook 2006).

A fifth specimen collected by Michaux and kept at P (Drake collection) consists of two upper shoots (Fig. 5) and bears a label "Solidago odora Hort Kew" and "Michaux" in black ink and "Herb. Richard" in red ink. These shoots are all identified by the first author as *Solidago tortifolia* Ell., having leaf shape and small leaf margin serrations typical of that species.

The first herbarium sheet (P00320362) with the Michaux handscript is selected here as the lectotype of *Solidago retrorsa* Michx. The second (P02512809) and third (P02512861) sheets include possible isolectotypes or possible syntypes of *S. retrorsa*. The fourth (P00320365) and fifth (P02512864) herbarium sheets do not contain any type material of *S. retrorsa* because the specimens belong to another *Solidago* species. The name *Solidago retrorsa* belongs in synonymy under *S. odora* Ait., the oldest valid name for the species.

Solidago retrorsa Michx. in Flora Boreali-Americana (Michaux) 2: 117. 1803. **LECTOTYPE** (designated here): **USA**. Basse Caroline, Bois pres l'habitat, *A. Michaux s.n.* (P00320362!-Fig. 1; possible isolectotypes/syntypes: P02512809!-Fig. 2, P02512861!-Fig. 3)

Solidago retrorsa was listed by Rafinesque (1836) in his protologue of *Solidago* subg. *Triactis* Raf. The protologue was brief: "Triactis. Rad. 3-4 brevis cuneatis, flosculis 3-5. Typ. 1 *S. retrorsa* Mx. 2. *tortifolia* E." Nesom (1993) selected *S. tortifolia* as the lectotype for *Solidago* subg. *Triactis,* but our interpretation is that Rafinesque designated *S. retrorsa*, a synonym of *S. odora*, as the type species. The numbering of all species listed under the various subgenera was consecutive and species listed after other subgenera were not in alphabetical order. Thus, we take the first species listed following "Typ." as Rafinesque's type for each subgenus, not the other species designated as lectotypes by Nesom (1993).

Figure 3. Possible isolectotype/syntype of *Solidago retrorsa* Michx. *Michaux s.n.* (P). Barcode: P02512861. <https://science.mnhn.fr/institution/mnhn/collection/p/P02512861>

Figure 4. *Solidago odora* collection that is *S. tortifolia*. *Michaux s.n.* (P-MICHX). Barcode: P00320365. <https://science.mnhn.fr/institution/mnhn/collection/p/item/P00320365>

Figure 5. *Solidago odora* collection that is *S. tortifolia*. *Michaux s.n.* (P). Barcode: P02512864. <https://science.mnhn.fr/institution/mnhn/collection/p/P02512864>

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A MULTIVARIATE STUDY OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. IV. THE *SOLIDAGO PUBERULA* COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

The *Solidago puberula* complex is considered to include four species in *Solidago* subsect. *Squarrosae*. **Solidago puberula** and **Solidago pulverulenta** have sometimes been treated as conspecific (at varietal or subspecific rank) but here are separated. **Solidago roanensis** has very short hairs on the upper stems similar to those of the first two, but is glabrous to very sparsely hairy proximally. **Solidago sciaphila** has been considered closely similar to *S. speciosa* and *S. hispida* or possibly to *S. roanensis*. Among these four, multivariate analyses indicate that *S. sciaphila* is the most distinct and *S. puberula* and *S. pulverulenta* are the most similar.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes 14 species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017a). Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2020 frequently updated) has recognized 15 species: *S. bicolor* L., *S. erecta* Pursh, *S. georgiana* Semple, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond. Semple et al. (2017a) included a multivariate analysis of 14 species of subsect. *Squarrosae* emphasizing members of the *S. speciosa* complex; in their first analysis *S. puberula*, *S. pulverulenta*, *S. roanensis* and *S. sciaphila* formed a peninsula of taxa on the third canonical axis. Semple et al. (2017b) reported the results of the multivariate study of the *S. bicolor*-*S. hispida* complex. Semple et al. (2017c) described *S. georgiana* and reported the results of a multivariate analysis of the larger-headed species of the subsection plus *S. roanensis*.

The *Solidago puberula* complex consists of four species — *S. puberula* (Figs. 1-2) and *S. pulverulenta* (Figs. 3-4) and more distantly *S. roanensis* (Figs 5-6 in Semple et al. 2017b) and *S. sciaphila* (Figs 7-8 in Semple et al. 2017b). Both *S. puberula* and *S. pulverulenta* have stems that are covered in a dense indument of very short curved hairs (Figs. 2C-D, 4C) and phyllaries that are always linear lanceolate with acute elongated tips in *S. puberula* (Fig. 2G) and similarly so (Figs. 4E-F) or sometimes less so in *S. pulverulenta*. Both are known only at the diploid level ($2n$=18; Beaudry & Chabot 1959; Beaudry 1969; Kapoor 1970; Morton 1981; Semple et al. 1984, 1993; Semple & Chmielewski 1987; Semple & Cook 2004; unpublished data). *Solidago roanensis* is also known only at the diploid level ($2n$=18; Beaudry 1963; Semple et al. 1984; Semple et al. 2015; Semple et al. 2019), while *S. sciaphila* is known only at the tetraploid level ($2n$=36; Semple et al. 2015; unpublished data).

The ranges of distribution and the locations of specimens included in the analyses are shown for *Solidago puberula* and *S. pulverulenta* in Figure 5. The ranges of distribution and the locations of specimens included in the multivariate analyses for *S. roanensis* and *S. sciaphila* were shown in Figures 13-14 of Semple et al. (2017b), respectively. The range of *S. sciaphila* is near the driftless area of the Mississippi River drainage and surrounding areas and does not overlap with any of the other three, while the ranges of the other three are variously sympatric in the central and the southern

Figure 1. Morphology of *Solidago puberula*. *Semple & B. Semple 11456* (WAT) from New Brunswick.

Figure 2. Details of the morphology of *Solidago puberula*. **A-D, F-G.** Morton & Venn NA12493 (JKM in ROM). **A-B.** Basal rosette leaves and leaf margin. **C-D.** Lower stem. **E.** Upper stem leaf, Morton & Venn NA12622 (JKM in ROM). Figure 2. Details of the morphology of Solidago puberula. A-D, F-G. Morton & Venn NA12493 (JKM in ROM). A-B. Basal rosette leaves and leaf margin. C-D. Lower stem. E. Upper stem leaf, Morton & Venn NA12622 (JKM in ROM). F-G. Portion of Inflorescence and heads. Scale bars = 1 cm in A-B and E; = 1 mm in C-D and F-G. Portion of Inflorescence and heads. Scale bars = 1 cm in A-B and E; = 1 mm in C-D and F-G.

Figure 3. Morphology of *Solidago pulverulenta*. *Kral 33682* (MO) from Covington Co., Alabama.

Figure 4. Details of the morphology of *Solidago pulverulenta*. **A.** Small shoot, cropped from *Rodgers 340* LSU00137215_L.JPG, Florida; used with permission. **B.** Basal rosette leaves, *Kral 33682* (MO), Alabama. **C.** Lower stem, *Semple 11635* (WAT), North Carolina. **D.** Mid stem leaves, *Kral 44276* (WAT), Alabama. **E.** Upper stem leaves, *Kral 33682* (MO). **F.** Heads, *Semple 11597* (WAT), North Carolina. **G.** Heads, *Kral 41621* (MO), Alabama. **H.** Cypselae with old corollas, *Ahles 37731* (NCU), South Carolina. Scale bars = 1 dm in A, 1 cm in B, D-E; = 1 mm in C, E-G.

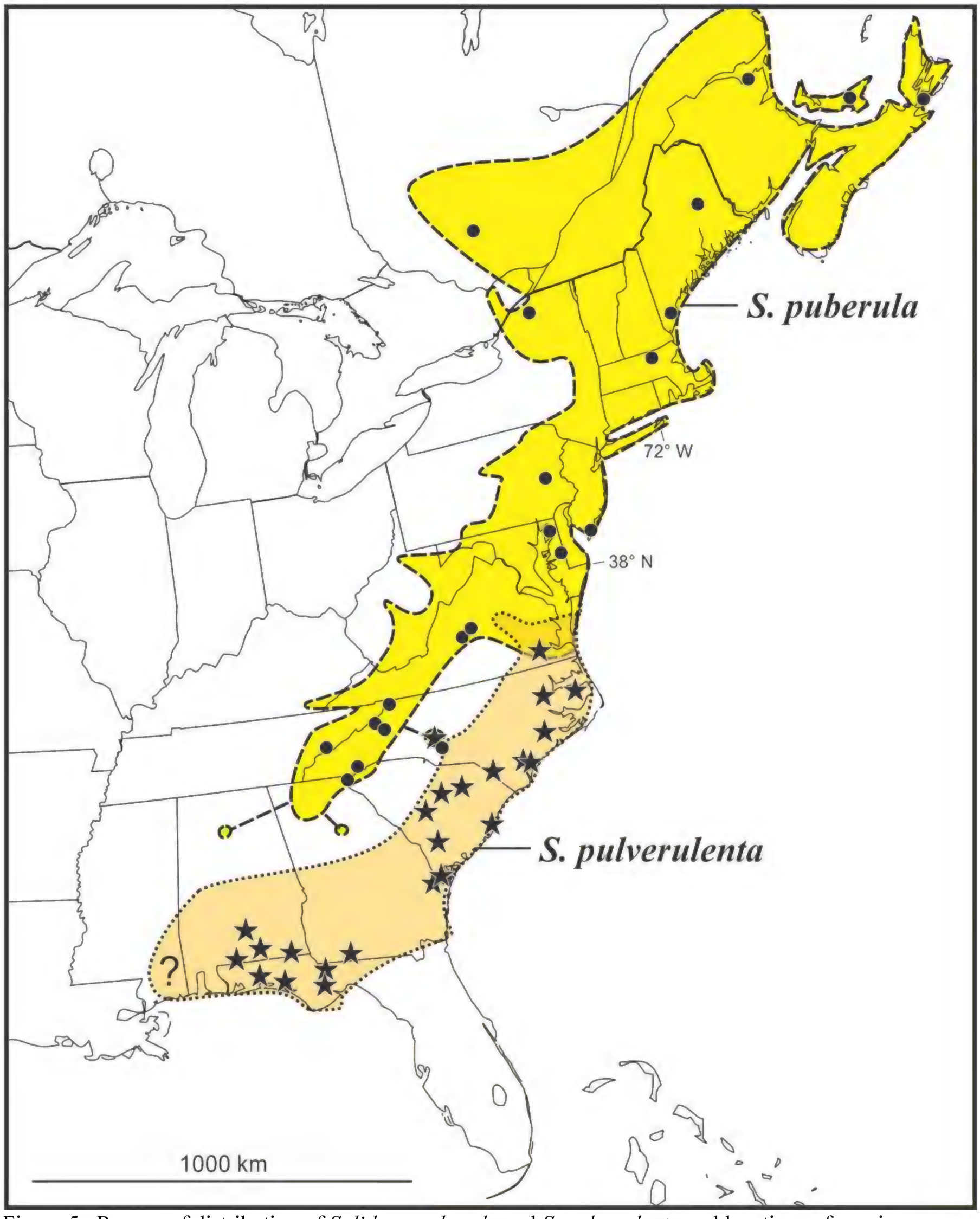

Figure 5. Ranges of distribution of *Solidago puberula* and *S. pulverulenta* and locations of specimens included in the multivariate analyses (no vouchers seen to confirm presence of *S. pulverulenta* in Mississippi or Louisiana; vouchers seen were misidentified specimens of *S. nemoralis*).

Appalachian Mountains (*S. roanensis* and *S. puberula*), along the edge of the Piedmont in North Carolina (*S. puberula* and *S. pulverulenta*), and where the Atlantic and Southern Coastal Plains come

together in southeastern Virginia (*S. puberula* and *S. pulverulenta*). Most of the ranges of *S. puberula* and *S. pulverulenta* are allopatric.

Solidago pulverulenta has been treated as *S. puberula* var. *pulverulenta* (Nutt.) Chapm. and as *S. puberula* subsp. *pulverulenta* (Nutt.) Semple. Torrey and A. Gray (1942) treated the taxon at the species rank in the first Flora North America, while Semple and Cook (2006) treated the taxon as a subspecies in the second Flora North America. Fernald (1950) treated the taxon as a variety of *S. puberula* as did Cronquist (1968, 1980) and Radford et al. (1968). Weakley (2015) treated the taxon at species rank. Small (1903) treated *S. puberula* and *S. pulverulenta* as species distinguished by involucres being turbinate-campanulate, 2.5 mm thick for *S. pulverulenta* versus involucres being narrowly campanulate, 3 mm thick for *S. puberula*. Mackenzie in Small (1933) keyed out the two species as follows: "blades of the leaves about the middle of the stem oblong-obovate, hispidulous above all over: inner involucral bracts gradually narrowed, oblanceolate nearly 1 mm wide" in *S. puberula* and "blades of the leaves about the middle of the stem oblanceolate, strongly hispidulous above on mid rib, slightly so elsewhere; inner involucral bracts rather abruptly narrowed above middle, very narrowly lanceolate, about 0.5 mm wide" in *S. pulverulenta*. Mackenzie in Small (1933) listed *S. puberula* as occurring from Florida to Mississippi north to Québec and Prince Edward Island and noted in the description that the phyllaries veins were obsolete in *S. puberula* and obscure in *S. pulverulenta*. Semple and Cook (2006) keyed out subsp. *puberula* as having "leaves 20–50(–60), mid cauline usually 40–50 mm; phyllaries attenuate; Nova Scotia to Ontario, s to piedmont and mountains in Georgia", while subsp. *pulverulenta* had "leaves (20–)50–110+, mid cauline 10–40 mm; phyllaries acute to barely attenuate; coastal plain, se Virginia to n Florida, w to e Louisiana." Weakley (2015) separated the two species as follows: *S. puberula* had leaves 20-50 (-60) per stem, midstem leaves usually 4-5 cm long, and phyllaries attenuate; and *S. pulverulenta* had leaves (20-) 50-120 per stem, midstem leaves usually 1-4 cm long, and phyllaries acute to acuminate.

The objectives of this study were to determine which morphological traits best separate the taxa of the *Solidago puberula* complex and to determine the most appropriate nomenclatural rank for the taxa. No detailed multivariate analysis of the complex has been previously published, although specimens of *S. puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila* were included in the overall analysis of subsect. *Squarrosae* in Semple al. (2017a).

MATERIALS AND METHODS

In total, 87 specimens from BOON, GA, LSU, MIN, MO, NCU, NY, TAWES, J.K. Morton personal herbarium now in TRT, and WAT in MT (Thiers, continuously updated) were scored and included in the analysis: *Solidago puberula* (25 specimens), *S. pulverulenta* (24 specimens), *S. roanensis* (20 specimens), and *S. sciaphila* (18 specimens). These were selected from more than 400 hundred specimens examined. For each specimen, 18 vegetative and 15 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 1. In addition, stem hair densities were rated for the lower, mid, and upper stem and used for identification purposes.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology are presented in Semple et al. (2016) and are not repeated here. Four analyses were performed. In the first analysis, four species of subsect. *Squarrosae* were included in a STEPWISE discriminant analysis. In the second and third analyses, three species of subsect. *Squarrosae* were included in STEPWISE discriminant analyses. In the fourth analysis, the two core species of the *Solidago puberula* complex were included in a STEPWISE discriminant analysis.

Table 1. Traits scored for the multivariate analyses of 261 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
LONGBRLN	Length of the longest lower inflorescence branches (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
IPHYLN	Inner phyllary length (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret achene length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

RESULTS

Four Species Level Groups Analysis

The Pearson correlation matrix yielded $r > |0.7|$ for most pairs of leaf traits reducing the number to be used to either mid leaf length, mid leaf width, and mid leaf serrations and sometimes upper leaf width and serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: lower stem leaf length, petiole length, width, and length from widest point to

tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. The numbers of ray florets and disc florets were sometimes highly correlated and only one trait was used in the analyses. Ray floret ovary/fruit body length at anthesis correlated highly with disc floret ovary/fruit body length and only the latter trait was included in the discriminant analyses. Ray floret pappus length at anthesis and disc floret pappus length at anthesis were highly correlated and only the latter was used in the discrimiant analyses. Inflorescence length and lower inflorescence branch length correlated highly and were generally used in defining a priori groups and were not included in the analyses.

In the STEPWISE discriminant analysis of 87 specimens of four species level a priori groups (*Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila*), the following six traits were selected and are listed in order of decreasing F-to-remove values: mid leaf length (13.36), disc floret ovary/fruit body length at anthesis (13.28), mid leaf width (11.84), number of upper leaf margin serrations (8.06), ray floret lamina length (4.91), and disc floret corolla length (4.73). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. pulverulenta* and *S. roanensis* (30.531); the smallest separation was between *S. puberula* and *S. pulverulenta* (5.386).

In the Classificatory Discriminant Analysis of the four species level a priori groups (*Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 70-83%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Fifteen of the 18 specimens of the *S. sciaphila* a priori group (83%) were assigned a posteriori into the *S. sciaphila* group; 11 specimens with 90-100% probability, 1 specimen with 86% probability, 1 specimen with 77% probability, and 1 specimen with 65% probability. Three specimens of the *S. sciaphila* a priori group were assigned a posteriori to other species: 2 specimens to *S. roanensis* with 66% probability (19% to *S. sciaphila* and 12% to *S. puberula*; *Smith 14978* MIN from Houston Co, Minnesota: and 1 specimen with 34% probability to S. *roanensis*; *Smith 14982A* MIN from Houston Co., Minnesota); 1 specimen to *S. pulverulenta* with 51% probability (26% to *S. puberula*, 14% to *S. roanensis* and 9% to *S. sciaphila*). Nineteen of the 24 specimens of *S. pulverulenta* a priori group (79%) were assigned a posteriori to the *S. pulverulenta* group; 6 specimens with 90-97% probability, 6 specimens with 85-89% probability, 4 specimens with 73-79% probability, and 7 specimens with 60-65% probability. Five specimens of the *S. pulverulenta* a priori group were assigned a posteriori to *S. puberula*: 64% probability (33% to *S. pulverulenta*; *Semple 11635* WAT from Pender Co., North Carolina; 108 cm tall shoot with 77 stem leaves), 58% probability (42% to *S. pulverulenta*; *Massey 3129* NCU from Sussex Co., Virginia; a 100+ cm tall shoot with many stem nodes and a large long branches inflorescence and a flowering branch arising ca. 50 cm below the apex), 55% probability (44% to *S. pulverulenta*; *Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), 52% probability (48% to *S. pulverulenta*; *Bell 10884* NCU from Florence Co., South Carolina; a 77 cm tall shoot with 58 nodes below the inflorescence), and 52% probability (47% to *S. pulverulenta*; *Radford 42490* NCU from Tyrrell Co., North Carolina; 57 cm tall shoot with ca. 45 nodes below the inflorescence). Nineteen of 25 specimens of the *S. puberula* a priori group (76%) were assigned a posteriori to the *S. puberula* group: 61 specimens with 93-100% probability, 3 specimens with 81-84% probability, 4 specimens with 70-76% probability; 2 specimens with 68-69% probability, 3 specimens with 55% probability (45% to *S. pulverulenta*; *Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82

cm tall shoot ca. 51 leaves below the inflorescence), 54% probability (44% to *S. pulverulenta*; *Duncan 10356* GA from Rabun Co., Georgia; 70 cm tall shoot with ca. 24 stem leaves below the inflorescence), and 54% probability (46% to *S. pulverulenta*; *Freye 8037* TAWES from Cecil Co., Maryland; 47 cm tall shoot with ca. 23 stem leaves below the inflorescence), and 1 specimen with 38% probability (*Cook et al. C-561* WAT from Transylvania Co., North Carolina; 42.6 cm tall shoot with ca. 22 leaves below the inflorescence). Six specimens of the *S. puberula* a priori group were assigned a posteriori to the other species: 5 specimens to *S. pulverulenta* with 70% probability (30% to *S. puberula*; *Freer 12280* NC from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), 68% probability (32% to *S. puberula*; *Semple & B. Semple 11479* WAT from Queens Co., Prince Edward Island; 67 cm tall shoot with 22 stem leaves below the inflorescence), 63% probability (33% to *S. puberula*; *Cook & Seiden C-124* WAT from Reserve la Verendrye, Québec; 73.6 cm tall shoot with ca. 28 stem leaves below the inflorescence), and 50% probability (49% to *S. puberula*; *Freer 12280* NC from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), and; and 1 specimen to *S. roanensis* with 57% probability (26% to *S. puberula and 13% to S. sciaphila*; *Semple & Suripto 9586* WAT from York Co., Maine; lower stem finely puberulent). Fourteen of the 20 specimens of the *S. roanensis* a priori group (70%) were assigned a posteriori to the *S. roanensis* group: 10 specimens with 91-100% probability, 2 specimens with 64-65% probability, and 2 specimen with 56% probability (31% to *S. sciaphila* and 9% to *S. puberula*; *Morton & Venn NA6471* WAT from Swain Co., North Carolina) and 51% probability (43% to *S. sciaphila* and 5% to *S. puberula*; *Williams s.n.* NY from Clay Co., North Carolina). Six specimens of the *S. roanensis* a priori group were assigned a posteriori to the other species, all had glabrous/glabrate lower stems and mid and inner phyllaries with multiple veins: 4 specimens to *S. sciaphila* with 93% probability (*Biltmore Herb. 4622* NY from Buncombe Co., North Carolina), 74% probability (*Cannon 213* NY from Avery Co., North Carolina), 68% probability (*Kral 62768* NY from Polk Co., Tennessee), and 57% probability (31% to *S. roanensis*; Cook *et al. C-557* WAT from Haywood Co., North Carolina); and 2 specimens to *S. puberula* with 86% probability (*Poindexter 05-1580* BOON from Ashe Co., North Carolina) and 52% probability (18% to *S.* sciaphila, 15% to *S. roanensis*, and 15% to *S. pulverulenta*; Cook *et al. C-557* WAT from Haywood Co., North Carolina).

Table 2. Between groups F-matrix for the three a priori group analysis (df = 5 56).

Group	*puberula*	*pulverulenta*	*roanensis*
pulverulenta	5.386		
roanensis	23.030	30.531	
sciaphila	20.505	20.885	8.395

Wilks' lambda = 0.1098 df = 6 3 83; Approx. F= 18.5333 df = 18 221 prob = 0.0000

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	*puberula*	*pulverulenta*	*roanensis*	*sciaphila*	% correct
puberula	19	5	1	0	76
pulverulenta	5	19	0	0	79
roanensis	2	0	14	4	70
sciaphila	0	1	2	15	83
Totals	26	25	17	19	77

Jackknifed classification matrix

Group	*puberula*	*pulverulenta*	*roanensis*	*sciaphila*	% correct
puberula	19	5	1	0	76
pulverulenta	5	19	0	0	79
roanensis	2	1	12	5	60
sciaphila	1	1	2	14	78
Totals	27	26	15	19	74

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 87 specimens of *Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila* are presented in Figure 6. Eigenvalues on the first three axes were 3.171, 0.770, and 0.233.

Three Species Level Groups Analysis I: *Solidago puberula*, *S. pulverulenta*, and *S. sciaphila*

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid leaf length, width, and serrations and sometimes upper leaf width and serrations. Basal rosette and lower stem leaves were often/sometimes absent and were not included in the discriminant analyses. The numbers of ray florets and disc florets were highly correlated and only former trait was used in the analyses. Ray floret ovary/ cypsela body length at anthesis correlated highly with disc floret ovary/ cypsela body length at anthesis and only the latter trait was included in the discriminant analyses.

In the STEPWISE discriminant analysis of 63 specimens of three species level a priori groups in (*Solidago puberula*, *S. pulverulenta*, and *S. sciaphila*), the following five traits were selected and are listed in order of decreasing F-to-remove values: disc floret ovary/fruit body length at anthesis (31.25), upper leaf width (29.78), upper leaf length from widest point to apex (23.17), mid stem leaf length (15.78), and number of ray florets (6.32). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. pulverulenta* and *S. sciaphila* (54.235); the smallest separation was between *S. puberula* and *S. pulverulenta* (9.204).

Table 5. Between groups F-matrix for the three a priori group analysis (df = 5 56).

Group	*puberula*	*pulverulenta*
pulverulenta	0.924	
sciaphila	46.123	54.235

Wilks' lambda = 0.0880 df = 5 6 60; Approx. F= 26.5489 df = 10 112 prob = 0.0000

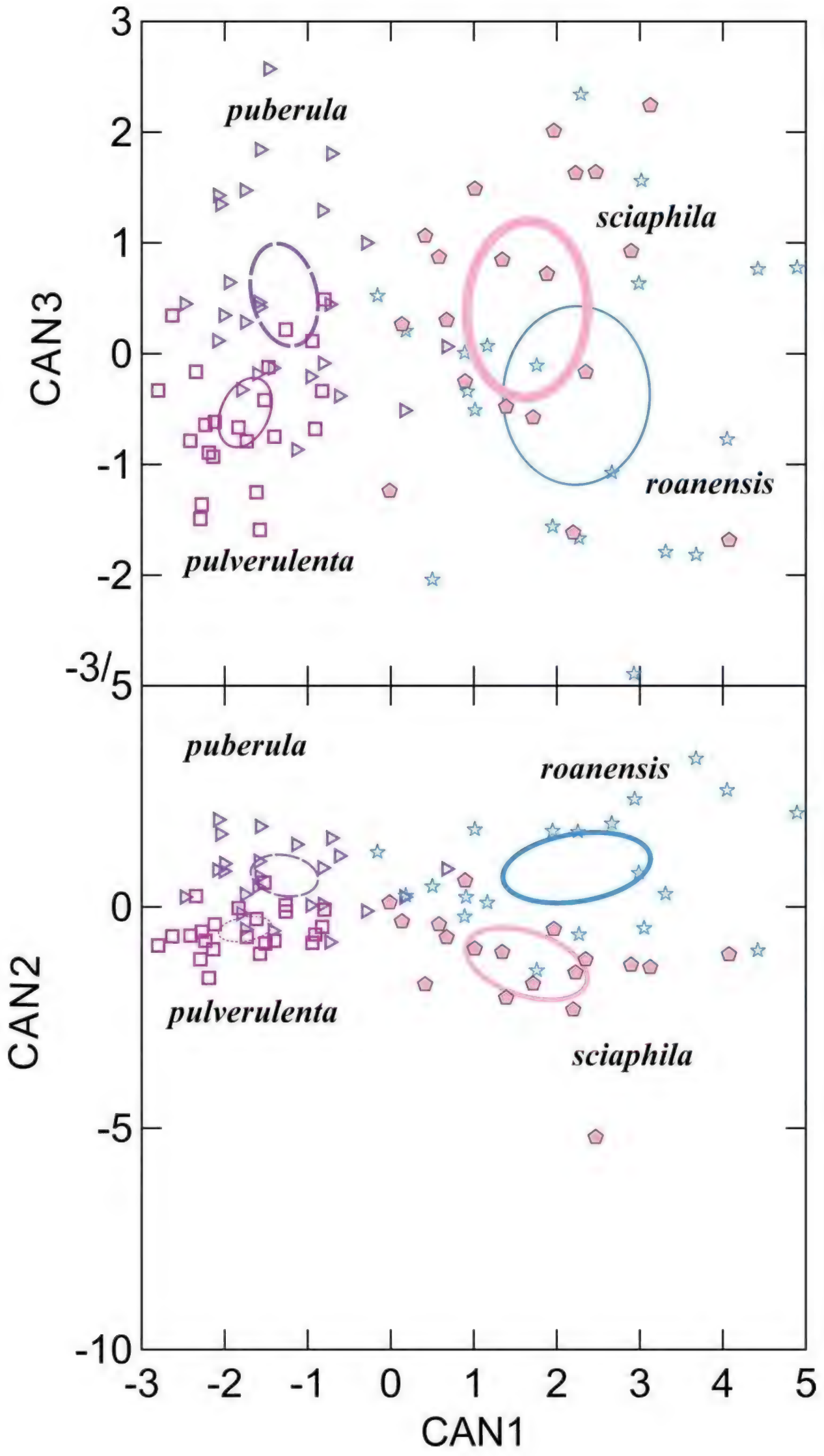

Figure 6. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 876 specimens of *Solidago* subsect. *Squarrosae*: *S. puberula* (open purple right oriented triangles), *S. pulverulenta* (magenta squares), *S. roanensis* (open blue stars), and *S. sciaphila* (pink pentagons); symbols match those in Fig 11 in Semple et al. 2017a.

In the Classificatory Discriminant Analysis of the three species level a priori groups (*Solidago puberula*, *S. pulverulenta*, and *S. sciaphila*), percents of correct a posterori assignment to the same a priori group ranged from 76-83%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. Fifteen of the 15 specimens of the *S. sciaphila* a priori group (100%) plus two specimens only included a posteriori were assigned a posteriori into the *S. sciaphila* group; 16 specimens with 100% probability and 1 specimen with 84% probability. One specimen of the *S. sciaphila* not included in the *S. sciaphila* a priori group in this analysis was assigned a posteriori to *S. pulverulenta* with 65% probability (35% to *S. puberula*; *Semple 11854* WAT from Carroll Co., Illinois; 16 cm tall shoot with ovate mid stem leaves with many obvious margin serrations; tetraploid). Twenty-one of the 24 specimens of the *S. pulverulenta* a priori group (88%) were assigned a posteriori to the *S. pulverulenta* group: 16 specimens with 90-98% probability and 5 specimens with 80-86% probability. Three specimens of the *S. pulverulenta* a priori group were assigned a posteriori to *S. puberula* with 90% probability (10% to *S. pulverulenta*; *Massey 3129* NCU; from Sussex Co., Virginia; a 100+ cm tall shoot with many stem nodes and a large long branches inflorescence and a flowering branch arising ca. 50 cm below the apex), 82% probability (*Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), and 66% probability (34% to *S. pulverulenta*; *Semple 11635* WAT from Pender Co., North Carolina; 108 cm tall shoot with 77 stem leaves). Twenty of the 24 specimens of the *S. puberula* a priori group were assigned a posteriori to the *S. puberula* group: 11 specimens with 90-100%, 5 specimens with 82-88% probability, 1 specimen with 72% probability, 1 specimen with 62% probability, and two specimens with 57% probability (43% to *S. pulverulenta*; *Bell 15176* NCU from Burke Co., North Carolina; 63 cm tall shoot with ca. 40 stem leaves below the inflorescence) and 53% probability (47% to *S. pulverulenta*; *Ahles & Leisner 19614* NCU from Cabarrus Co., North Carolina; 50 cm tall shoot with ca. 33 stem leaves below the inflorescence). Four specimens of the *S. puberula* a priori group were assigned a posteriori to *S. pulverulenta* with 86% probability (*Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82 cm tall shoot ca. 51 leaves below the inflorescence), 84% probability (*Semple & B. Semple 11479* WAT from Queens Co., Prince Edward Island; 67 cm tall shoot with 22 stem leaves below the inflorescence), 84% probability (*Freye 8037* TAWES from Cecil Co., Maryland; 47 cm tall shoot with ca. 23 stem leaves below the inflorescence), and 70% probability (*Freer 12280* NCU from from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence).

A two dimensional plots of CAN1 versus CAN2 canonical scores for 63 specimens of *Solidago puberula*, *S. pulverulenta*, and *S. sciaphila* are presented in Fig. 7. Eigenvalues on the first two axes were 5.397 and 0.776.

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*puberula*	*pulverulenta*	*sciaphila*	% correct
puberula	20	4	0	83
pulverulenta	3	21	0	88
sciaphila	0	0	15	100
Totals	23	25	15	89

Jackknifed classification matrix

Group	*puberula*	*pulverulenta*	*sciaphila*	% correct
puberula	20	4	0	83
pulverulenta	3	21	0	88
sciaphila	0	0	15	100
Totals	23	25	25	89

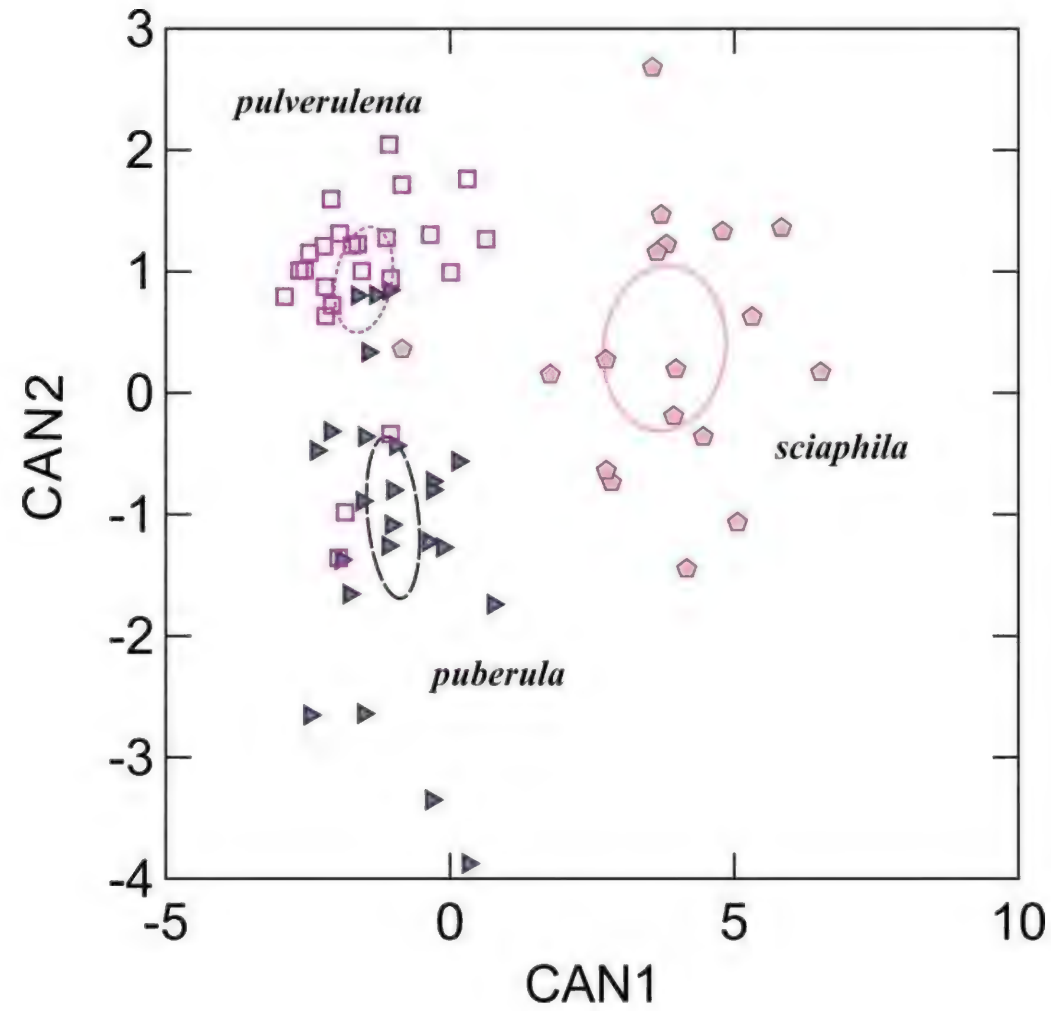

Figure 7. Plot of canonical scores (CAN1 vs CAN2) for 63 specimens of *Solidago puberula* (right-oriented purple triangles), *S. pulverulenta* (magenta squares), and *S. sciaphila* (pink pentagons).

Three Species Level Groups Analysis II: *Solidago puberula*, *S. pulverulenta*, and *S. roanensis*

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to upper leaf width and serrations. Basal rosette and lower stem leaves were often/sometimes absent and were not included in the discriminant analyses. The numbers of ray florets and disc florets were highly correlated and only former trait was used in the analyses. Ray floret ovary/ cypsela body length at anthesis correlated highly with disc floret ovary/ cypsela body length at anthesis and only the latter trait was included in the discriminant analyses.

In the STEPWISE discriminant analysis of 67 specimens of three species level a priori groups in (*Solidago puberula*, *S. pulverulenta*, and *S. roanensis*), the following four traits were selected and are listed in order of decreasing F-to-remove values: number of upper leaf margin serrations mid leaf length (11.94), disc floret ovary/fruit body length at anthesis (11.33), disc floret corolla length (6.93), and ray floret lamina length (5.71). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 7. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. pulverulenta* and *S. roanensis* (32.441); the smallest separation was between *S. puberula* and *S. pulverulenta* (3.863).

Table 7. Between groups F-matrix for the three a priori group analysis (df = 5 56).

Group	*puberula*	*pulverulenta*
pulverulenta	3.863	
roanensis	30.180	32.441

Wilks' lambda = 0.2243 df = 4 2 64; Approx. F= 16.9496 df = 8 122 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups (*Solidago puberula*, *S. pulverulenta*, and *S. roanensis*), percents of correct a posterori assignment to the same a priori group ranged from 70-83%. The Classification matrix and Jackknife classification matrix are presented in Table 8. Results are presented in order of decreasing percents of correct placement. Sixteen of the 19 specimens of the *S. roanensis* a priori group (84%) plus 1 additional specimen included a posteriori were assigned a posteriori into the *S. roanensis* group; 12 specimens with 98-100% probability, 2 specimens with 89% and 81% probabilities, 1 specimen with 72% probability, 1 specimen with 67% probability, and 1 specimen with 55% probability (23% to *S. puberula* and 22% to *S. pulverulenta*; *Morton & Venn NA6471* WAT from Swain Co., North Carolina). Three specimens of the *S. roanensis* a priori group were assigned to other species, all had glabrous/glabrate lower stems and oligoneurate mid and inner series phyllaries: 2 specimens to *S. pulverulenta* with 77% probability (15% to *S. puberula* and 8% to *S. roanensis*; 227) and 72% (26% to *S. puberula*; 108); and 1 specimen to *S. puberula* with 57% probability (40% to *S. pulverulenta*; *Williams s.n.* NY from Clay Co., North Carolina). Nineteen of the 24 specimens of the *S. pulverulenta* a priori group (79%) were assigned a posteriori into the *S. pulverulenta* group; 1 specimen with 90% probability, 3 specimens with 87-89% probability, 7 specimen with 70-79% probability, 4 specimens with 63-67% probability, and 4 specimens with 57% probability (42% to *S. puberula*; *Nelson & Desportes 9973* USCH from Georgetown Co., South Carolina; 69 cm tall shoot with damaged stem), 54% probability (46% to *S. puberula*; *Bell 10884* NCU from Florence Co., South Carolina; a 77 cm tall shoot with 58 nodes below the inflorescence), 54% probability (46% to *S. puberula*; *Bell 5327* NCU from Jasper Co., South Carolina; 81 cm tall shoot with ca. 74 stem leaves below the inflorescence), and 51% probability (49% to *S. puberula*; *Radford 41825* NCU from Martin Co., North Carolina; 78 cm tall shoot with more than 55 stem leaves below the inflorescence). Five specimens of the *S. pulverulenta* a priori group were assigned to *S. puberula* with 75% probability (25% to *S. pulverulenta*; *Rodgers 338* LSU from Okaloosa Co., Florida; 78 cm tall shoot with ca. 80 stem leaves below the inflorescence), 71% probability (27% to *S. pulverulenta*; *Semple 11635* WAT from Pender Co., North Carolina; 108 cm tall shoot with 77 stem leaves), 59% probability (41% to *S. pulverulenta*; *Radford 42490* NCU from Tyrrell Co., North Carolina; 57 cm tall shoot with ca. 45 nodes below the inflorescence), 57% probability (43% to *S. pulverulenta*; *Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), 54% probability (45% to *S. pulverulenta*; *Kral 41668* WAT from Geneve Co., Alabama; 108 cm tall shoot with ca. 66 stem leaves below the inflorescence). Thirteen of the 24 specimens of the *S. puberula* a priori group (54%) were assigned a posteriori into the *S. puberula* group; 4 specimens with 91-95% probability, 2 specimens with 89% and 86% probabilities, 2 specimens with 77% probability each, 2 specimens with 61% probability each, and 3 specimens with 56% probability (44% to *S. pulverulenta*; *Bell 15176* NCU from Burke Co., North Carolina; 63 cm tall shoot with ca. 40 stem leaves below the inflorescence), 56% probability (43% to *S. pulverulenta*; *Freer 12280* NCU from from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence),

and 54% probability (46% to S. pulverulenta; *Semple & B. Semple 11479* WAT from Queens Co., Prince Edward Island; 67 cm tall shoot with 22 stem leaves below the inflorescence). Eleven specimens of the *S. puberula* a priori group were assigned to other species: 9 specimens to *S. pulverulenta* with 72% probability (28% to *S. puberula*; *Freer 12297* NCU from Nelson Co., Virginia; 72 cm tall shoot with ca. 41 leaves below the inflorescence), 71% probability (29% to *S. puberula*; *Stewart s.n.* NCU from Transylvania Co., North Carolina; 52.5 cm tall shoot with ca. 37 leaves below the inflorescence), 70% probability (30% to *S. puberula*; *Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82 cm tall shoot ca. 51 leaves below the inflorescence), 56% probability (42% to *S. puberula*; *Duncan 10356* GA from Rabun Co., Georgia; 70 cm tall shoot with ca. 24 stem leaves below the inflorescence), 55% probability (45% to *S. puberula*; *Morton & Venn NA17622* TRT from Piscataquis Co., Maine; 87 cm tall shoot with 38 leaves below the inflorescence), 55% probability (45% to *S. puberula*; *Cook & Seiden C-124* WAT from Reserve la Verendrye, Québec; 73.6 cm tall shoot with ca. 28 stem leaves below the inflorescence), 53% probability (47% to *S. puberula*; *Poindexter 09-1113* NCU from Alleghany Co., North Carolina; 87 cm tall shoot with ca. 46 leaves below the inflorescence), 52% probability (48% to *S. puberula*; *Morton & Venn NA16106* TRT from Cape May Co., New Jersey; 79 cm tall shoot with ca. 55 leaves below the inflorescence), and 50% probability (50% to *S. puberula*; *Ahles & Leisner 19614* NCU from Cabarrus Co., North Carolina; 50 cm tall shoot with ca. 33 stem leaves below the inflorescence); and 2 specimens to *S. roanensis* with 63% probability (27% to *S. puberula* and 10% to *S. pulverulenta*; *Cook et al. C-561* WAT from Transylvania Co., North Carolina; 42.6 cm tall shoot with ca. 22 leaves below the inflorescence) and 60% probability (20% to *S. puberula* and 19% to *S. pulverulenta*; *Semple & Suripto 9586* WAT from York Co., Maine; lower stem finely puberulent).

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*puberula*	*pulverulenta*	*roanensis*	% correct
puberula	13	9	2	54
pulverulenta	5	19	0	79
roanensis	1	2	16	84
Totals	26	25	19	77

Jackknifed classification matrix

Group	*puberula*	*pulverulenta*	*roanensis*	% correct
puberula	13	9	2	54
pulverulenta	7	17	0	71
roanensis	2	2	15	79
Totals	27	26	19	74

A two dimensional plot of CAN1 versus CAN2 canonical scores for 63 specimens of *Solidago puberula*, *S. pulverulenta*, and *S. roanensis* are presented in Fig. 8. Eigenvalues on the first two axes were 5.397 and 0.776.

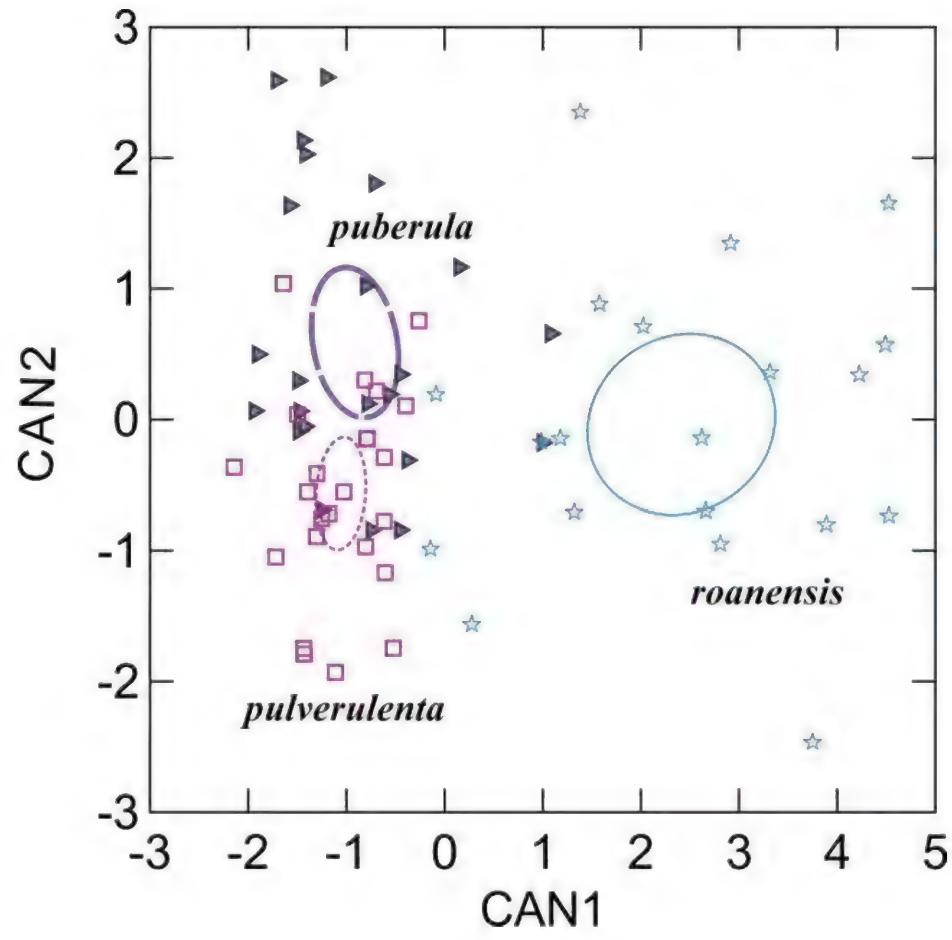

Figure 8. Plot of canonical scores (CAN1 vs CAN2) for 63 specimens of *Solidago puberula* (right-oriented purple triangles), *S. pulverulenta* (magenta squares), and *S. roanensis* (blue stars).

Two Species Level Groups Analysis: *Solidago puberula* and *S. pulverulenta*

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length and number of margin serrations and upper leaf width and number of margin serrations. Basal rosette and lower stem leaves were often/sometimes absent and were not included in the discriminant analyses. The numbers of ray florets and disc florets were highly correlated and only the former trait was used in the analyses. Ray floret ovary/ fruit body length at anthesis correlated highly with disc floret ovary/ fruit body length at anthesis and only the latter trait was included in the discriminant analyses.

In the STEPWISE discriminant analysis of 48 specimens of two species level a priori groups in (*Solidago puberula* and *S. pulverulenta*), the following three traits were selected and are listed in order of decreasing F-to-remove values: mid stem leaf length (23.30), involucre height (11.19), and disc floret corolla length (5.05). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. *Solidago puberula* and *S. pulverulenta* had an F-to separate value of 13.618 (Wilks' lambda = 0.5185 df = 3 1 46; Approx. F= 13.6177 df = 3 44 prob = 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups (*Solidago puberula* and *S. pulverulenta*), percents of correct a posterori assignment to the same a priori group were 83% for both groups. The Classification matrix and Jackknife classification matrix are presented in Table 7. Twenty of the 24 specimens of the *S. puberula* a priori group (83%) were assigned a posteriori into the *S. puberula* group; 10 specimens with 90-100% probability, 1 specimen with 89% probability, 5 specimens with 74-78% probability, 3 specimens with 62-64% probability, and 1 specimen with 59% probability (*Semple & Chmielewski 6227* WAT from Blount Co., Tennessee; 96 cm tall shoot with ca. 59 stem leaves below the inflorescence). Four specimens of the *S. puberula* a priori group were assigned a posteriori to *S. pulverulenta* with 81% probability (*Freer 12280* NCU from from Amherst Co., Virginia; 56.5 cm tall shoot with ca. 50 stem leaves below the inflorescence), 61% probability (*Freye 8037* TAWES from Cecil Co., Maryland; 47 cm tall shoot with ca. 23 stem leaves below the inflorescence), 56% probability (*Cook et al. C-561* WAT from Transylvania Co., North Carolina; 42.6 cm tall shoot with ca. 22 leaves below the inflorescence), and

53% probability (*Semple & Ringius 7638* WAT from Caroline Co., Virginia; 82 cm tall shoot ca. 51 leaves below the inflorescence). Twenty of the 24 specimens of the *S. pulverulenta* a priori group (83%) were assigned a posteriori into the *S. pulverulenta* group; 13 specimens with 92-99% probability, 1 specimen with 88% probability, 3 specimens with 72-78% probability, 1 specimen with 61% probability, and 2 specimens with 55% probability (*Radford 42490* NCU from Tyrrell Co., North Carolina; 57 cm tall shoot with ca. 45 nodes below the inflorescence) and 51% probability (*Kral 61116* MO from Calhoun Co., Florida; 85 cm tall shoot with a damaged inflorescence apex and ca. 63 leaf nodes below the inflorescence). Four specimens of the *S. pulverulenta* a priori group were assigned a posteriori to *S. puberula* with 90% probability (*Massey 3129* NCU from Sussex Co., Virginia; a 100+ cm tall shoot with many stem nodes and a large long branches inflorescence and a flowering branch arising ca. 50 cm below the apex), 78% probability (*Semple 11597* WAT from Rowan Co., North Carolina; 117 cm tall shoot with more than 75 stem leaves), 78% probability (*Ahles 37308* NCU from Robeson Co., North Carolina; 98 cm tall shoot with ca. 65 stem leaves below the inflorescence), and 50% probability (*Kral 41668* WAT from Geneve Co., Alabama; 108 cm tall shoot with ca. 66 stem leaves below the inflorescence).

Histograms of CAN1 frequencies for 63 specimens of *Solidago puberula* and *S. pulverulenta* are presented in Fig. 9. The Eigenvalue on the first axis was 0.776.

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	*puberula*	*pulverulenta*	% correct
puberula	20	4	83
pulverulenta	4	20	83
Totals	24	24	83

Jackknifed classification matrix

Group	*puberula*	*pulverulenta*	% correct
puberula	20	4	83
pulverulenta	5	19	79
Totals	24	23	81

DISCUSSION

The results of the multivariate analyses indicate that *Solidago puberula*, *S. pulverulenta*, and *S. roanensis* and *S. sciaphila* can be treated as separate species with *S. sciaphila* being the most distinct and *S. puberula* and *S. pulverulenta* being the most similar. The phylogenetic position of the tetraploid species *S. sciaphila* has not been determined by DNA sequence data but it is assumed to be either the basal member of the *S. puberula* complex clade or perhaps more closely related to *S. hispida* in the *S. bicolor/S. hispida* clade. Semple and Cook (2006) treated *S. puberula* and *S. pulverulenta* as conspecific subspecies within *S. puberula*. Weakley (2012) treated the two taxa as varieties within *S. puberula*. but as separate species in Weakley (2015).

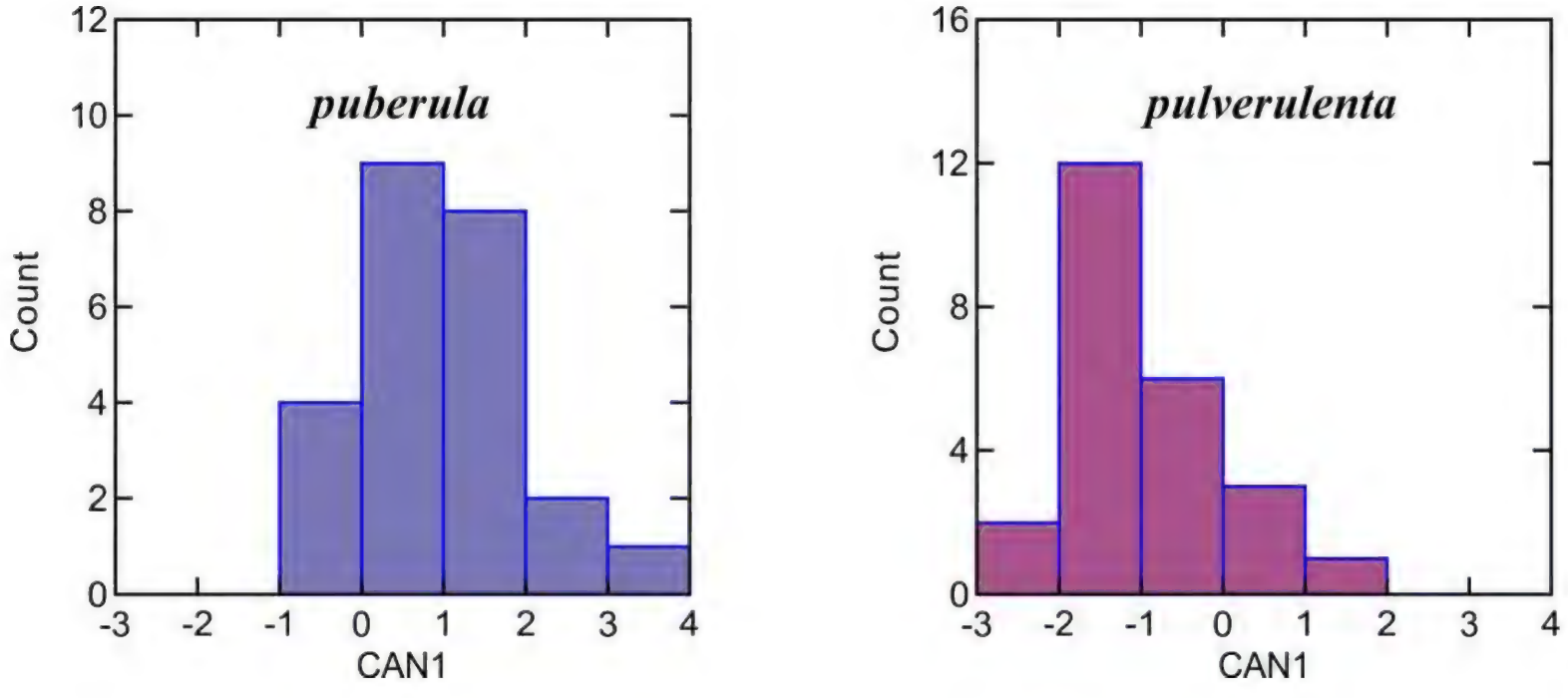

Figure. 9. Histograms of CAN1 canonical scores for 48 specimens of *S. puberula* (left) and *S. pulverulenta* (right).

The results of the third analysis indicate that *Solidago roanensis* is significantly different from *S. puberula* and *S. pulverulenta* on technical traits as well as the more obvious shift from glabrous/glabrate lower stem to increasing more densely short-canescent mid and upper stems. General leaf shape is similar in all three species being broadly to narrowly oblanceolate to lanceolate. There are obvious differences in the phyllaries with those of *S. roanensis* being less attenuate and with the mid and inner ones usually having 3 or more pronounced veins, while the phyllaries of *S. puberula* and *S. pulverulenta* are usually narrow and attenuate and single veined. The limited number of vegetative traits included in the analysis resulted in weak separate of *S. puberula* from *S. pulverulenta* with only 54% of the *S. puberula* specimens being assigned a posteriori to *S. puberula.*

The results of the first, second and fourth analysis indicate that there are significant differences between *Solidago puberula* and *S. pulverulenta* with the latter generally being more strongly supported. It can be argued that the two taxa do not differ sufficiently to warrant species status as was done by Semple and Cook (2006) in Flora North America where the two were treated as subspecies. The two taxa have also been treated as varieties within *S. puberula*, e.g., Cronquist (1980). The results of this study are not sufficiently strong to indicate that species level status is the only option.

Semple (1974) presented a discussion of subspecies, variety and form level ranks using *Xanthisma texanum* DC. as the example following the concepts of Ehrendorfer (1968). The subspecies concept was considered to have a strong allopatric element to its application and the ranges of *Solidago puberula* and *S. pulverulenta* are mostly allopatric and were thus treated as subspecies of *S. puberula* in Semple and Cook (2006). Varietal rank was for different races with mostly or completely sympatric ranges. During the intervening 46 years since 1974, the lack of consensus in North America on how to apply the subspecies rank has shifted with the school favoring subspecies as merely a grouping category gaining dominance over those who viewed it as like varietal rank but with a strong allopatric distribution. Asa Gray did not use subspecies and his varieties included both strongly allopatric races and much more or totally sympatric races. It is my observation that for many (likely the majority) of taxonomists in North America today, subspecies is just a grouping category and that this is significantly the result of proponents of the grouping category school having simply academically outbred the alternative group. Contributors to Flora North America and regional floras have been and are required to choose between using subspecies or varieties even when they would prefer to recognize both in a floristic treatment. Thus, continuing to

treat *S. pulverulenta* as a subspecies within *S. puberula* has become much more problematic now because the two taxon are clearly closely related but at the same time have ranges of distribution that indicate significant differences in adaptations to different habitats. Varietal rank is not sufficient to indicate the extent of difference between *S. puberula* and *S. pulverulenta* in terms of morphology and ecology. Stem height and the associated number of nodes (and leaves) on a stem are highly variable within the two species. The taller the stem, the more reduced in size the upper most leaves are, but this is more pronounced in *S. pulverulenta*. However, very short plants of *S. pulverulenta* from Florida were examined as part of this study resulting in these plants having very few leaves of very small size; e.g. *Rodgers 340* LSU (Fig. 4A). Such plants will key out to *S. puberula* because they are short and have few stem leaves but are just dwarf morphs of *S. pulverulenta*.

Key to *Solidago puberula*, *S. pulverulenta*, *S. roanensis*, and *S. sciaphila*.

1. Mid stem leaves lanceolate to ovate, usually with small and large serrations; native to bluffs of Mississippi R. and tributaries in SE Minnesota and adjacent Wisconsin, Illinois and Iowa ..... **Solidago sciaphila**

1. Mid stem leaves lanceolate to oblanceolate, serrations few, small or none; Nova Scotia and Québec south to northern Georgia and Alabama in the mountains and Piedmont and to Florida on the coastal plain

   2. Lower stems glabrous or glabrate, mid to upper stems increasingly finely canescent; mid to inner phyllaries usually oligoneurate; mid to higher elevations in Piedmont and Applachian Mts. from Pennsylvania to northern Georgia eastern Tennessee, and northeastern Alabama ..... **Solidago roanensis**

   2. Lower to upper stems densely finely canescent; phyllaries single veined, usually attenuate

      3. Leaves 20–50(–60), mid cauline usually 40–50 mm long, upper leaves somewhat reduced; phyllaries attenuate; Nova Scotia to Ontario south to Piedmont and mountains in Georgia (adjacent Alabama?) ..... **Solidago puberula**

      3. Leaves (20–)50–110+, mid cauline 10–40 mm long, upper leaves much reduced; phyllaries attenuate to acute; coastal plain, southeastern Virginia to northern and western Florida (possibly southern Mississippi and eastern Louisiana) ..... **Solidago pulverulenta**

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BURMEISTERA XINIAE (CAMPANULACEAE: LOBELIOIDEAE), UNA NUEVA ESPECIE ENDÉMICA DE LA CORDILLERA DE TALAMANCA EN COSTA RICA

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RESUMEN

Se describe e ilustra *Burmeistera xiniae* (Campanulaceae-Lobelioideae), una nueva especie endémica de la Cordillera de Talamanca en Costa Rica. Se compara con especies similares de Costa Rica, Panamá, Colombia, y Ecuador (*Burmeistera betancurii*, *B. caudatifolia*, *B. chiriquiensis, B. huacamayensis*, *B. maui*, y *B. truncata*) y se comenta su distribución, fenología y habitat.

ABSTRACT

Burmeistera xiniae (Campanulaceae-Lobelioideae), a new endemic species from the Cordillera de Talamanca of Costa Rica is described and illustrated. It is compared with similar species from Costa Rica, Panama, Colombia, and Ecuador (*Burmeistera betancurii*, *B. caudatifolia*, *B. chiriquiensis*, *B. huacamayensis*, *B. maui*, and *B. truncata*) and their distribution, phenology, and habitat are discussed.

Burmeistera H. Karst. & Triana fue descrita por los botánicos José Jerónimo Triana y Gustav Karl Wilhelm Hermann Karsten (Triana 1854; Karsten 1856) a partir de *Burmeistera ibaguensis* Triana & H. Karst., aunque sin asignar un espécimen tipo, por lo que fue apenas recientemente tipificado por Favio González y Javier Garzón (González & Garzón-Venegas 2015).

En este género se han registrado cerca de 120 especies (Garzón-Venegas & González 2012; Lagomarsino et al. 2015; González & Vélez-Puerta 2018; Rodríguez & Solano 2018; Vallejo et al. 2018; Mashburn et al. 2020). Es el cuarto más diverso de la subfamilia Lobelioideae, después de *Lobelia* L. con más de 400 especies, *Siphocampylus* Pohl con aproximadamente 230 especies y *Centropogon* C. Presl con cerca de 220 especies (Lammers 2007; González & Garzón 2015).

Burmeistera es un género endémico del Neotrópico que se registra en el sur de **México** (Chiapas) (1 spp.) (Stein 1987a; Rodríguez y Solano en prensa), **Honduras** (1 spp.) (Lammers y Maas 1998), **Guatemala** (1 spp.) (Nash 1976), **Costa Rica** (17 spp.) (Rodríguez y Solano en prensa), **Panamá** (21 spp.) (Lagomarsino et al. 2015), **Colombia** (ca. 60 spp.) (Garzón-Venegas y González 2012), **Ecuador** (ca. 40 spp.) (Jeppesen 1981; Vallejo et al. 2018; Mashburn et al. 2020) y **Perú** (2 spp.) (Stein 1987a). Se considera que la mayor diversidad de especies y endemismos se encuentra al norte de los Andes en Colombia y Ecuador, donde se ha registrado cerca del 75% de las especies y hasta seis distintas en una misma localidad, principalmente en elevaciones medias del bosque nuboso, entre 1500-2500 m, aunque comprende especies desde tierras bajas hasta zonas de páramo arriba de los 5000 m (Gleason 1925; Jeppesen 1981; Stein 1987a; Garzón-Venegas et al. 2014; Muchhala y Pérez 2015; Lagomarsino et al. 2016; Rodríguez y Solano 2018).

Este género se considera taxonomicamente bien delimitado, sin embargo, patrones morfológicos complejos, en particular la diferenciación local extrema, lo convierte en un desafío taxonómico a nivel de especie (Stein 1987a).

Se caracteriza por su hábito herbáceo o sufrútice (a veces arbustivos) o bejuco, terrestre, o epífito, con flores solitarias, que nacen usualmente entre las axilas de las hojas distales, caducas en frutos, los pedicelo usualmente ebracteolado, corola zigomorfa, verde a casi blanca o crema a amarilla (a veces teñida o rayada de rosado a rojo o rojizo a morado o marrón), o (menos frecuente) totalmente rosada a roja o morada a café claro, tubo de la corolla entero, nunca fenestrado o dorsalmente partido, lóbulos dorsales de la corolla más largos que los ventrales y falcados o reflexos, el tubo de las anteras ampliamente abierto en el ápice, y el ovario ínfero, y por sus frutos abayados, carnosos (esponjosos), en ocasiones inflados, con semillas oblongas a fusiformes, mucho más largas que anchas (Lammers 1998; Muchhala & Lammers 2005; Lagomarsino et al. 2015; Rodríguez & Solano en prensa).

Este género se encuentra relacionado a *Centropogon* C. Presl y *Siphocampylus* Pohl, ambos igualmente endémicos del Neotrópico (Gleason 1925; Lammers 1998; Antonelli 2008; Lagomarsino et al. 2014; Mashburn et al. 2020). *Burmeistera* se diferencia por mostrar pedúnculos por lo general ebracteados (vs. usualmente bibracteados), estilo, corola y estambres tempranamente deciduos y ausentes cuando en frutos (vs. estilo, corola y estambres tardíamente deciduos y con frecuencia persistentes en los frutos), el tubo formado por las anteras ampliamente abierto en el ápice (vs. dorso-ventralmente compreso y ocluido), anteras ventrales con el ápice glabro a esparcidamente piloso (vs. anteras ventrales con un penacho de tricomas setosos o apéndices triangulares en el ápice) y semillas oblongas a fusiformes (vs. elipsoides), además, al menos en Costa Rica son especies epífitas a ocasionalmente terrestres (vs. terrestres) (Lammers 1998; Muchhala y Pérez 2015; Rodríguez & Solano 2018; Mashburn et al. 2020). A la vez, *Siphocampylus* se diferencia de *Burmeistera* por sus frutos capsulares (loculicidas), apicalmente dehiscentes por dos valvas (vs. frutos abayados, carnosos o esponjosos e indehiscentes) (Lammers 1998; Muchhala & Pérez 2015; Rodríguez & Solano 2018). Adicionalmente en *Burmeistera*, con excepciones, predomina la polinización por murciélagos (Phyllostomidae), mientras que en *Centropogon* y *Siphocampylus* predomina la polinización por colibríes (Muchhala & Lammers 2005; Muchhala 2006).

La evidencia actual sugiere que *Burmeistera, Centropogon* y *Siphocampylus* en conjunto forman un solo clado, el que se caracteriza por su distribución Neotropical, hábito leñoso y tubo de la corolla entero, no fenestrado ni dorsalmente partido (Lammers 2002; Muchhala & Lammers 2005; Lagomarsino et al. 2015); mientras que de manera individual únicamente *Burmeistera* es monofilético (Knox et al. 2008; Antonelli 2008; Lagomarsino et al. 2014; Lagomarsino et al. 2015; Lagomarsino et al. 2016).

Wimmer (1932, 1943, 1968) dividió el género en dos secciones, *Barbatae* E. Wimm, con las dos anteras ventrales barbadas en el ápice, y la sección *Imberbes* (*nom. invalid* = sect. *Burmeistera* Lammers; ver Lammers 1998), con las cinco anteras glabras a esparcido-pubescentes en el ápice. Wimmer dividió la sección *Burmeistera* en dos subsecciones, pero Stein (1987b) transfirió los miembros de la subsección *Aequilatae* E. Wimmer al género *Siphocampylus* Pohl (Lammers 1998). En la actualidad esta clasificación en secciones se considera insatifactoria debido a que se basa en caracteres arbitrarios que no representa de la mejor manera la historia evolutiva de *Burmeistera* (Lammers 1998; Muchhala & Lammers 2005; Knox et al. 2008; Lagomarsino et al. 2014).

La revisión más completa para *Burmeistera* corresponde a la monografía realizada por Wimmer (1943), quien reconoció 77 especies. Luego se han publicado revisiones para varios países, eso incluye Guatemala (Nash 1976), Honduras (Lammers & Maas 1998), Costa Rica (Standley 1937; Wilbur 1975; Rodríguez & Solano en prensa), Panamá (Wilbur 1976, 1981), Ecuador (Jeppesen 1981) y Perú (Stein 1987a). Publicaciones adicionales que describen nuevas especies para el género se pueden encontrar

en Gleason (1925), McVaugh (1943, 1949a, 1949b, 1957, 1965), Wimmer (1955, 1968), Gómez & Gómez-Laurito (1986), Lozano & Galeano (1986), Luteyn (1986), Lammers (1998, 2002), Garzón-Venegas & González (2012, 2014), Garzón-Venegas, González & Vélez-Puerta (2012), Garzón-Venegas, Vélez-Puerta & González (2013), Garzón-Venegas, Luteyn & González (2014), Muchhala & Lammers (2005), Lagomarsino et al. (2015), Muchhala & Pérez (2015), González & Vélez-Puerta (2018), Rodríguez & Solano (2018), Vallejo et al. (2018) y Mashburn et al. (2020).

En *Burmeistera* las flores son protándricas y al menos en dos especies de Ecuador se ha demostrado que la antesis dura cerca de seis días. En la fase inicial masculina las anteras fusionadas forman un tubo dentro del que se desarrolla y alarga el estilo en tanto se libera el polen. Luego, la fase femenina se presenta cuando el suministro de polen se agota, el estigma emerge del tubo, se despliega y se vuelve receptivo (Muchhala & Jarrín 2002; Lagomarsino et al. 2015).

Las especies de *Burmeistera* están adaptadas casi universalmente para ser polinizadas por murciélagos que se alimentan de néctar, por lo que tienen adaptaciones florales características del síndrome quiropterolófilo, eso incluye antesis nocturna, flores de coloración opaca (por ejemplo verdes teñidas de morado o marrón), corola con morfología más campanulada, olor nocturno y una ubicación bien expuesta más allá de las hojas (Muchhala & Lammers 2005; Muchhala 2006; Muchhala & Pérez 2015). Estas especies adaptadas para polinización por murciélagos también podrían ser visitadas por colibríes, sin embargo, no transfieren de manera efectiva el polen. Los colibríes visitan las flores de *Burmeistera* temprano en la mañana y al anochecer (Feinsinger et al. 1987; Muchhala 2003), pero rara vez transportan polen y solo en pequeñas cantidades. Mientras que una sola visita de un murciélago depositará miles de granos en un estigma receptivo (Muchhala & Lammers 2005). Al menos una especies, *Burmeistera rubrosepala* (E. Wimm.) E. Wimm. de Ecuador, es exclusivamente polinizada por colibríes, y se caracteriza por sus flores con predominancia de coloración rojo brillante, sin olor, que abren en las tardes, con el tubo de la corola estrecho y tubular y con pedicelos flexibles que las colocan debajo del follaje o que apenas sobrepasan más allá de las hojas (Muchhala 2006; Muchhala & Jarrín 2002; Muchhala & Pérez 2015).

En la Cordillera de Talamanca, que se comparte entre Costa Rica y Panamá, se han registrado 25 especies de *Burmeistera*, la región con más alta diversidad después de los Andes (Lagomarsino et al. 2015; Rodríguez & Solano en prensa).

En Costa Rica se reportan 17 especies pertenecientes a este género, de las que 16 se han registrado en la Cordillera de Talamanca (considera únicamente el lado costarricense), siete son endémicas, algunas tienen distribución muy restringida o al menos se conocen de muy pocos especímenes y se distribuyen en bosque húmedo, muy húmedo, páramo y principalmente pluvial, entre 200-3300 m (Rodríguez & Solano 2018; Rodríguez & Solano en prensa).

Una reciente revisión de la familia Campanulaceae para el Manual de Plantas de Costa Rica (Rodríguez & Solano en prensa) ha resultado con el hallazgo de esta nueva especie de *Burmeistera* nativa y endémica de la Cordillera de Talamanca en Costa Rica. La especie exhibe una particular combinación de caracteres que permite proponerla como distinta de otras especies y nueva para la ciencia.

BURMEISTERA XINIAE Al. Rodr. & D. Solano, **sp. nov. TIPO**: **COSTA RICA**. Limón: Cantón de Talamanca, Cordillera de Talamanca, Cerro Carguicacha a Cerro Biricuacua, entre Ujarrás y San José Cabécar, 09°24´00” N, 83°10´40” W, 2200 m, 1 abril 1993 (flores y frutos), *G. Herrera 6126* (holotipo: CR-182671; isotipos: CR-1582606). Figuras 1A-L, 2A-D.

Burmeistera xiniae is recognized by the combination of the following characters: epiphytic, subscandent and hanging habit, leaves sometimes appearing to be subopposed by their often very short internodes, between 0.05–2.5 cm long, leaf blade linear to linear-lanceolate, 13–22.5 times longer than wide,

margin with 1–6 teeth per cm and with 10–17 pairs of secondary veins and evident submarginal veins, by its green corolla, sometime stained with fuchsia and uninflated fruits, fuchsia or lilac when ripe. This entity has been confused with *Burmeistera chiriquiensis* Wilbur, an endemic species from Panama, but the latter is distinguished by showing leaves loosely arranged on the stem and not appearing subopposed, with generally more elongated internodes, between 1–3 cm, leaf blade 10–15 times longer than wide, almost indistinct secondary and submarginal veins and margin with 1–2 teeth per cm, and by their flowers with a more elongated staminal column, ca. 23 mm (vs. 7–9 mm).

Hierba epífita, ca. 1.5 m, subescandente y colgante; tallo sufruticoso, 1–4 mm de diámetro, fistuloso, subterete, con 6–8 costillas inconspicuas que salen 2 de la base de cada pecíolo, una a cada lado, glabro, en material vivo verde teñido de fucsia, cuando seco pajizo, entrenudos 0.05–2.5 cm de largo (hojas a veces pareciendo subopuestas). Hojas espiralmente arregladas; pecíolo 0.2–1 cm de largo, glabro, ascendentes, a veces divaricado o (en hojas proximales) con frecuencia reflexo; lámina 4.5–11 cm de largo y 0.4–0.8 cm de ancho, linear-lanceolada a linear, 13–22.5 veces más larga que ancha, distales con lámina que se reduce ligeramente en forma y tamaño, base corto-cuneada, ápice estrecho y largamente acuminado, margen denticulado, rara vez dentado o bidentado, a irregular y gruesamente dentado, dientes calloso-glandulares, con 1–6 dientes por cm (en hojas maduras), nervadura conspicua, con 10–17 pares de nervios secundarios y el nervio submarginal evidente, haz y envés glabros, concoloros a leve-discoloros, con el lado abaxial ligeramente más pálido. Flores solitarias, axilares en nudos subterminales; pedúnculo 30–95 mm de largo, glabro, ebracteado, ascendente a casi péndulo; hipantio en la antesis obcónico a urceolado, 6–8.5 mm de largo y 2–4 mm de ancho, glabro, verde teñido de fucsia, con 10 nervios longitudinales ligeramente impresos, ecarinado; cáliz 5-lobulado, lóbulos ascendentes, subiguales a ligeramente más cortos que el hipantio, 2.5–8 mm de largo y 1–1.5 mm de ancho, subiguales a (ocasionalmente) desiguales en tamaño, lanceolados, oblongos a oblongo-lanceolados, verde fucsia, ápice agudo, subenteros a 1–4-dentados, inconspicuo-nervados, glabros a glabrescentes; corola 13–20 mm de largo, externamente esparcida e inconspicuo-pubescente a glabrescente, internamente glabra, verde, comunmente teñida de fucsia (especialmente hacia la base), ventricosa en la antesis, tubo de 4.5–9 mm de largo (hasta el lóbulo ventral) y 1.5–3.5 mm de ancho, lóbulos falcados, con el ápice agudo, dorsales 5.5–10 mm de largo, laterales 4.5–6 mm de largo, ventral 3.5–5 mm de largo; columna estaminal 7–9 mm de largo (no incluye las anteras) y 0.7–1 mm de ancho, subigual en largo o más corta que la corola, 1/3–3/4 de su largo basal glabrescente, 1/3–2/3 de largo distal esparcida y cortamente blanco pubescente, filamentos connatos hasta cerca de la base, adnatos a la corola cerca de la base; anteras con el tubo 3–3.5 mm de largo y 1.5–2 mm de ancho, esparcidamente blanco pubescentes, especialmente las dorsales, las 2 anteras ventrales 2.5–3 mm de largo, el ápice esparcidamente ciliado a pronto glabrescente o glabro, con tricomas blancos y pilosos de 0.6–0.9 mm de largo, las 3 anteras dorsales 4.5–5 mm de largo. Frutos 0.5–0.8 de largo y 0.5–0.7 cm de ancho, ovoides a globosos, carnosos (esponjosos), no inflados, fucsia o lila al madurar, glabros, exocarpo de consistencia subcoriacea a membranácea; semillas 0.6–0.8 de largo y 0.3–0.5 mm de ancho, elipsoides, subcilíndricas a bicovexas, reticuladas, pajizas.

Fenología. Flores y frutos recolectados en abril.

Distribución y hábitat. Endémica de Costa Rica. Crece en los bosques pluviales de la vertiente Caribe en la Cordillera de Talamanca, entre el Cerro Carguicacha a Cerro Biricuaca, 2200-2600 m.

Etimología. El epíteto latino *xiniae* fue dado en honor a la Dra. Xinia Peralta Ballester (año de nacimiento: 1950), madre de Daniel Solano y coautor de esta publicación, a quien con mucho cariño y aprecio se le dedica el nombre de esta especie. Xinia es microbióloga con estudios de posgrado en inmunología, máster en educación, bachiller en música y escritora de cuentos infantiles. Aparte de brindarnos su afecto, a menudo nos apoya con financiamiento para realizar expediciones botánicas.

Especímenes adicionales examinados. COSTA RICA. Limón. Talamanca, Cordillera de Talamanca, Flanco NE y cumbre Cerro Biricuacua, entre Ujarrás y San José Cabécar, 09°23´55" N, 83°10´10" W, 2600 m, 2 abril 1993 (flores), *Herrera 6164* (CR-187144; CR-1582879).

Discusión. *Burmeistera xiniae* se reconoce por la combinación de los siguientes caracteres: hábito epífito, subescandente y colgante, hojas a veces pareciendo subopuestas por sus entrenudos con frecuencia muy cortos, entre 0.05–2.5 cm de largo, la lámina foliar linear-lanceolada a linear, 13–22.5 veces más larga que ancha, el margen con 1–6 dientes por cm y la nervadura con 10–17 pares de nervios secundarios, el nervio submarginal evidente, flores con corola verde, comunmente teñida de fucsia (especialmente hacia la base) y frutos carnosos (esponjosos), no inflados, fucsia o lila al madurar.

Esta entidad ha sido confundida con *Burmeistera chiriquiensis* Wilbur, una especie endémica de Panamá y con la que presenta gran similitud, sin embargo, esta última se distingue por mostrar hojas laxamente dispuestas sobre el tallo y no pareciendo subopuestas, con entrenudos por lo general más alargados, entre 1–3 cm, lámina foliar entre 10–15 veces más larga que ancha, nervios secundarios y el submarginal casi indistintos (vs. conspicuos) y el margen con 1–2 dientes por cm, y por sus flores con una columna estaminal más alargada, ca. 23 mm (vs. 7–9 mm).

También, similar a *Burmeistera caudatifolia* Al. Rodr. & D. Solano, endémica de Costa Rica, y *B. maui* D. Solano & Al. Rodr., de Costa Rica y Panamá. Estas especies se distinguen por mostrar hojas laxamente dispuestas sobre el tallo y no pareciendo subopuestas (entrenudos 0.3–4 cm), lámina foliar entre 1.9–10.75 veces más larga que ancha, y flores con la corola, los lóbulos dorsales y laterales y la columna estaminal más alargados; además, en *B. maui* sobresale que a veces las hojas tiene el margen grueso-dentado a pinnatifido (para detalles y diferencias adicionales ver Cuadro 1).

Otras especies fenotípicamente similares son *Burmeistera betancurii* Garzón & F. González, endémica de Colombia, *B. huacamayensis* Jeppesen, endémica de Ecuador, y *B. truncata* Zahlbr., registrada de Colombia y Ecuador. Pesentan similitud con *B. xiniae* en caracteres como partes vegetativas glabras a glabradas, hojas con la lámina a menudo más o menos estrecha y con el ápice distintivamente alargado, por sus flores con la corola verde y a veces teñida de marrón, rojo púrpura, morado o fucsia y por sus frutos carnosos (esponjosos) no inflados. En general, estas especies se diferencian por mostrar tallos con entrenudos bien diferenciados, entre 1–3.7 cm de largo, hojas no pareciendo subopuestas, con la lámina comunmente más ensanchada, entre 0.5–3.5 cm (vs. 0.4–0.8 cm) y entre 3.5–7 veces más larga que ancha. Diferencias adicionales se pueden notar en el Cuadro 1.

Carácter	*B. betancurii*	*B. caudatifolia*	*B. chiriquiensis*	*B. huacamayensis*	*B. maui*	*B. truncata*	*B. xiniae sp. nov.*
Entrenudos: largo (cm)	1.5-3	0.9-4	1-3	1-3	0.3-3	1.5-3.7	0.05-2.5
Hojas: largo y ancho (cm) de lámina	(9-)12-14(-16) × 2-3.5	6-12 × 0.7-3.5	6-12.5 × 0.4-1	9-14 × 2-3.5	3-10.5 × 0.7-2.5	7-12 × 2-3	4.5-11 × 0.4-0.8
Hojas: relación del largo vs. el ancho	3.5-5.5	2.5-10	10-15	4.5-7	1.9-10.75	3.5-4.5	13-22.5
Hojas: margen (dientes/cm)	1-2	1-3	1-8	1-2	1–9	1-2	1-6
Hojas: pares de nervios secundarios	7-9	7-13	11-21	12-16	10-21	12-13	10-17
Lóbulos del cáliz: largo (mm) y margen	1.5-2.5, entero	2.5-5, entero	2.5-5.5(-9), subentero a 1-3-dentados	4-6, entero	2.5-10.5, subentero a 1-4-dentado	8-15, entero	2.5-8, subentero a 1-4-dentado
Corola: color	verde, a veces teñida de marrón	verde teñida de rojo púrpura	verde teñida de púrpura oscuro	verde con violeta	verde teñida de morado púrpura	verde, a veces teñida de marrón	verde, comúnmente teñida de fucsia
Corola: largo (mm)	38-42	23-26	12-24	30-31	23-30	ca. 25	13-20
Corola: largo de lóbulos dorsales (mm)	18-25	11-12	11-13	ca. 14	10-14	ca. 16	5.5-10
Corola: largo de lóbulos laterales (mm)	13-15	6.5-8	ca. 7	ca. 9	6-10	ca. 8	4.5-6
Corola: largo del lóbulo ventral (mm)	8-10	4-5	ca. 5	ca. 9	4-10	7-8	3.5-5
Columna estaminal: largo (mm)	32	19-20	ca. 23	24-26	19-25	ca. 30	7-9
Anteras dorsales: largo (mm)	7-9	4-4.5	ca. 4.5	5-6	5-7	8.1	4.5-5
Frutos: largo y ancho (cm)	1.5-2.5 × 1-1.5	0.6-1 × 0.5-0.8	ca. 0.9 × 0.7	0.9-1.5 × 0.9-1.3	1–1.7 × 0.8–1.7	Sin datos	0.5-0.8 × 0.5-0.7

Cuadro 1. Características diferenciales entre *B. xiniae* con especies similares. Medidas y caracteres de *B. betancurii, B. huacamayensis* y *B. truncata* tomados de Garzón-Venegas y González (2012); *B. caudatifolia* y *B. maui* de Rodríguez y Solano (2018); y *B. chiriquiensis* de Wilbur (1976).

Figura 1. *Burmeistera xiniae*. A. Hábito con flores y frutos. B. Hoja. C. Detalle del margen y la nervadura de la hoja. D. Detalle del tallo y base de la hoja. E. Botón floral. F. Flor en vista lateral externa. G. Lóbulo del cáliz. H. Flor en vista lateral interna. I. Anteras. J. Fruto. K. Semilla. L. Detalle de superficie de la semilla. A-B, F, J-L de *Herrera 6126* (CR-182671); C de *Herrera 6164* (CR-187144); D, G *Herrera 6164* (CR-1582879); E, H-I de *Herrera 6126* (CR-1582606).

Figura 2. *Burmeistera xiniae*. A. Hábito. B. Hojas. C. Flor. D. Fruto. Fotografías por D. Solano, sin testigo.

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ESTADO DE CONSERVACIÓN DE *THEOBROMA CACAO* EN COSTA RICA

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RESUMEN

El cacao (*Theobroma cacao* L.) es una especie nativa de la zona tropical de América, sin embargo, su origen y domesticación ha sido tema de debate debido a las diversas propuestas y discrepancias entre autores. En Costa Rica, el cacao ha sido documentado en estado silvestre por distintos botánicos a través de los años, no obstante, esta evidencia aislada no ha permitido determinar su estado de conservación, por tanto, el objetivo de esta investigación es describir el estado de conservación de *Theobroma cacao* para Costa Rica. Se revisó la totalidad de especímenes de cacao recolectados en el país y depositados en los herbarios CR, MO y USJ para determinar la cantidad de poblaciones naturales conocidas. La evaluación del estado de conservación de la especie se efectuó con base en la metodología propuesta por la IUCN. Se encontró un total de nueve posibles poblaciones naturales del cacao, de las cuales ocho se localizan en la vertiente Pacífica húmeda y una población en el Caribe. Se adiciona con este estudio una nueva posible población natural en Cuesta de Pita de Potrero Grande, Buenos Aires. Con base en los criterios de conservación de las especies de IUCN, sugerimos que *T. cacao* es una especie que se puede clasificar como Vulnerable. Este trabajo robustece la importancia de la documentación de flora en los bosques primarios del país, con el fin de establecer bases científicas para la conservación del entorno natural y sus especies.

ABSTRACT

The origin and domestication of cacao (*Theobroma cacao L.)* have been the subject of debate. All cocoa specimens collected in Costa Rica and deposited in the CR, MO, and USJ were reviewed to determine the number of known natural populations. Nine possible natural populations were found, of which eight are located on the humid Pacific slope and one population in the Caribbean. A new possible natural population in Cuesta de Pita de Potrero Grande, Buenos Aires, is added in this study. Based on the IUCN species conservation criteria, we suggest that *T. cacao* can be classified as Vulnerable in Costa Rica.

La especie *Theobroma cacao* L., popularmente conocida como cacao, es un árbol nativo de las zonas tropicales de América (Miranda, 1962). Es ampliamente cultivado para la producción del popular cacao y sus derivados. Se cultiva bajo la sombra de otros árboles permitiendo su nicho el establecimiento diversas especies de organismos, la conexión entre ecosistemas y áreas productivas agrícolas, así como zona de amortiguamiento (Krasuss et al. 2003, Suatunce et al. 2003).

Desde su formal descripción por Carl von Linnaeus (1753), es conocido que esta especie se distribuye en el Neotrópico, sin embargo, su origen y domesticación ha sido tema de debate debido a las propuestas y discrepancias entre diversos autores. Según Motamayor (2002), la concepción de la idea de que el origen del cacao es Sudamericano es recurrente entre muchos autores y constantemente se afirma que procede de las cuencas de los ríos Amazonas y Orinoco y en los valles de sus afluentes, no obstante, se sostiene que el centro de cultura y domesticación del cacao fue Centroamérica. Por su parte, Shultes (1984) difiere al proceso de domesticación, afirmando que la especie se distribuye naturalmente solo en Sudamérica y se extendió a Centroamérica por medio de la migración de indígenas. Lo anterior de igual forma concuerda con lo expuesto por Motamayor (2002) que expone que no existen poblaciones nativas auténticas en la región de México y Centroamérica, a pesar de haber sido cultivo durante 2000 años, sugiriendo que el cacao fue introducido a esta zona (Chesman 1944).

La historia del cacao en Costa Rica es extensa. Su documentación inicia con el reporte de Juan Vásquez de Coronado en el año 1563 sobre su cultivo en el cantón de Quepos, Puntarenas. Luego, el auge comercial del cacao en el país inicia hasta el año 1650 y extendiéndose hasta 1800 (MacLeod 1996). A nivel geográfico, la región del Caribe ha sido una de las zonas con mayor producción de cacao en el país, especialmente en las tierras bajas de Talamanca, no obstante, existe en menor grado cultivos en Puntarenas en la vertiente Pacífica (Keithan 1940).

Diversos botánicos han recolectado muestras de cacao silvestre en varias partes del país, las cuales se encuentran depositadas en los herbarios nacionales e internacionales. Algunas de estas muestras provienen de diferentes localidades boscosas del país y representan probablemente poblaciones nativas, las cuales están en su mayoría alejadas de cultivos y regiones ampliamente pobladas en la actualidad. Según Rodríguez (2015), dichas localidades constituyen baja Talamanca en la vertiente caribe, y Parque Nacional Carara, Parque Nacional La Cangreja y la Península de Osa en la vertiente pacífica. A pesar de esta evidencia, se desconoce el estado de las poblaciones naturales, así como su estado de conservación. Por lo tanto, el objetivo de esta investigación es documentar las poblaciones posiblemente naturales de *Theobroma cacao* en Costa Rica.

MATERIALES Y MÉTODOS

Se revisó la totalidad de especímenes de cacao recolectados en el país que están depositados en los herbarios CR, MO y USJ para determinar la cantidad de posibles poblaciones naturales, así como también aquellas muestras provenientes de plantaciones o asentamientos humanos. Los especímenes provenientes de plantaciones o plantas cultivadas están indicados en las etiquetas del propio espécimen. Aquellos especímenes que no indican el hábitat de recolecta (*A. Tonduz* s.n., *CR3927* [1891], *A Tonduz* s.n., *CR6615* [1892], *A Tonduz* s.n., *CR9928* [1986]), no fueron incluídos en el análisis pues no se menciona más que el nombre de la localidad y no el hábitat de recolecta. La evaluación del estado de conservación de la especie se efectuó con base en la metodología propuesta por la IUCN (IUCN 2012, IUCN Standards and Petitions Subcommittee, 2017). El mapa se llevó a cabo mediante la revisión de 34 especímenes de herbario. Cada punto en el mapa refleja fielmente cada recolecta con su coordenada específica, con excepción de aquellos especímenes que no indicaban las coordenadas los cuales fueron georreferenciados estableciendo una ubicación aproximada con la información disponible de la etiqueta.

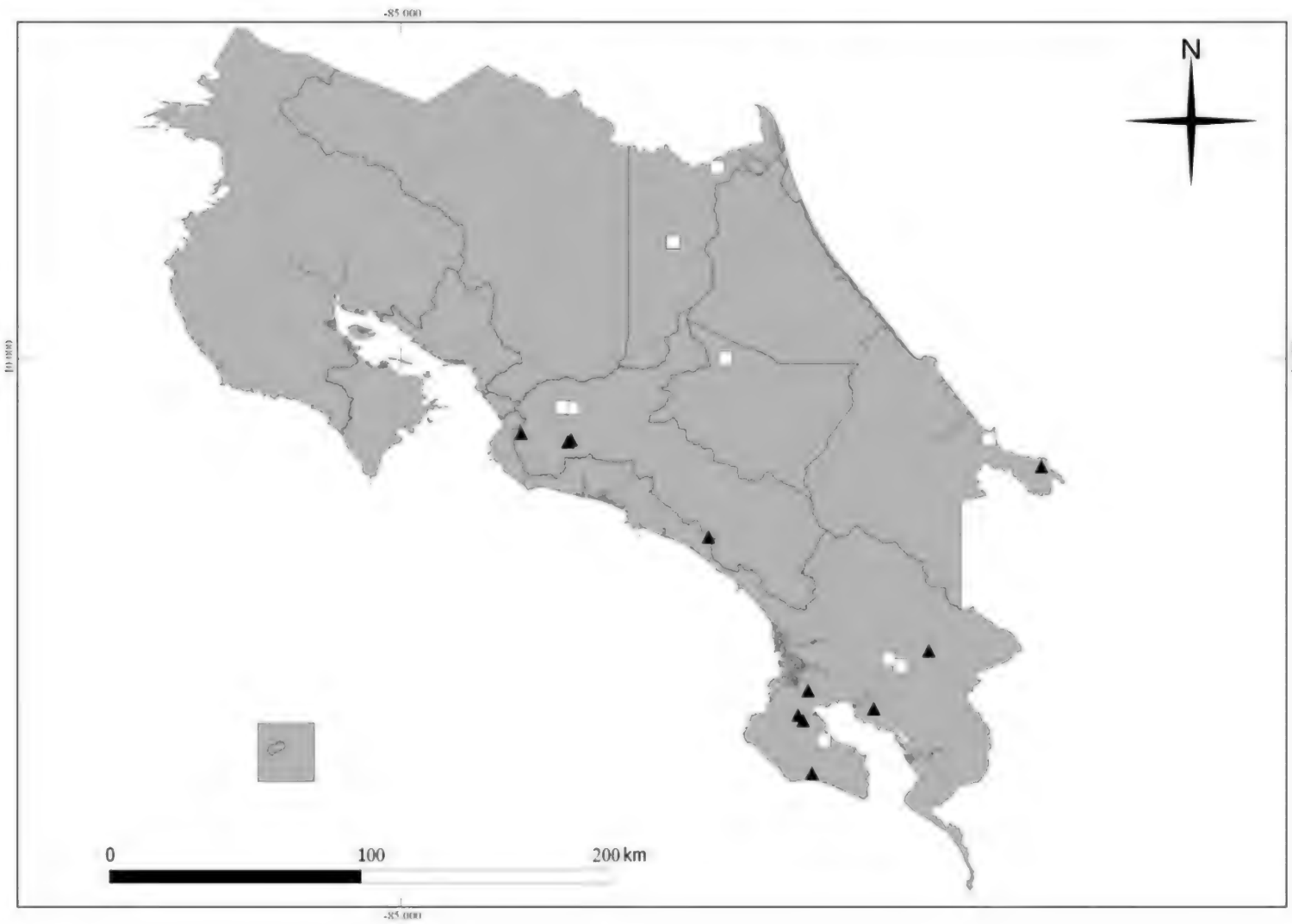

Figura 1. Distribución de las posibles poblaciones naturales (triángulos) y cultivadas (cuadros) de *Theobroma cacao* en Costa Rica.

Figura 2. Bosque primario en la región de cuesta de Pita, con especies que superan los 85 cm de diámetro y 30 m de diámetro.

Figura 3. Individuos de *Theobroma cacao* en Cuesta de Pita, Buenos Aires de Puntarenas (*M. Cedeño, J.E Jiménez & M. López 1708*). A. Rama con hojas dispuesta en forma dística. B. Flor desarrollándose en el tallo principal. C. Flor desarrollándose en las ramas. D. Frutos inmaduros desarrollados en las ramas, 10-acostillados y el ápice inclinado hacia un lado.

RESULTADOS Y DISCUSIÓN

Se encontró un total de nueve posibles poblaciones naturales de *Theobroma cacao* en el país, proveniente del análisis de 34 especímenes de herbario relacionados con esta especie. Un total de 26 especímenes proviene de plantaciones mientras que trece especímenes corresponden a las posibles poblaciones naturales (Fig. 1). La mayoría de las poblaciones naturales están localizadas en el bosque húmedo tropical de las tierras bajas de la vertiente Pacífica, con excepción de una población en la vertiente Caribe, específicamente en Manzanillo, Limón. Los especímenes recolectados sugieren que, sin excepción, todas las poblaciones se encuentran dentro de bosques primarios o bosques primarios intervenidos.

Una de las poblaciones naturales es de recién descubrimiento en una isla de bosque primario de aproximadamente 30 hectáreas en la región de Potrero Grande de Buenos Aires de Puntarenas, específicamente en la localidad de Cuesta de Pita. En la población se observaron nueve individuos con una altura promedio de 10–14 m y un diámetro de 20 cm. Estos árboles tienen un fuste recto, poco o sin ramificaciones basales, hasta los 3 m de altura, luego desarrollan ramas laterales. Dichos individuos fueron observados con frutos el 13 de julio del 2019 y con flores el 23 de abril del 2020

(Figura 2). El testigo botánico de su hallazgo se encuentra depositado en el herbario de la Universidad de Costa Rica (*Cedeño, Jiménez, & López 1708*, USJ). El bosque primario donde fue encontrada esta población se encuentra dominado principalmente por árboles de *Anacardium excelsum* (Bertero & Balb. Ex Kunth) Skeels (Anacardiceae), *Virola koschnyi* Warb. (Myristicaceae), *Brosimum costaricanum* Liebm., y *Brosimum lactescens* (S. Moore) C.C. Berg (Moraceae) (Figura 3).

De acuerdo con Rodríguez (2005), las poblaciones de cacao silvestre en Costa Rica difieren morfológicamente de los grupos cultivados por los frutos 10-acostillados (vs. 5-acostillados), el ápice cónico o piramidal e inclinado hacia un lado, y sus semillas con el embrión blanco (vs. morado).

Estado de conservación

Theobroma cacao en Costa Rica esta resguardada en cinco de las nueve posibles poblaciones naturales en el país, las cuales se encuentran protegidas en Parque Nacional Carara (52 km^2), Parque Nacional La Cangreja (25.7 km^2), Parque Nacional Corcovado (425.6 km^2), Parque Nacional Piedras Blancas (147 km^2) y Reserva Forestal Golfo Dulce (619 km^2). La extensión total donde se encuentra protegida la especie es de 1269.3 km^2. Con base a los criterios de la UICN, esta especie debe categorizarse como Vulnerable por tener una ocurrencia limitada menor a diez poblaciones conocidas en el país que ocupan un área menor a 2000 km^2 [B2ab(i,ii,iii,iv)] (IUCN 2012; IUCN Standards and Petitions Subcommittee 2017).

A pesar de que sugerimos categorizar esta especie bajo el estado de conservación Vulnerable, es indispensable analizar el estado in-situ de las poblaciones con el fin de conocer la abundancia y dominancia de la especie y brindar datos más robustos para la conservación de la especie.

Especímenes de *Theobroma cacao* proveniente de posibles poblaciones naturales

COSTA RICA. **Limón**: Manzanillo [Talamanca], range of hills ca. 2 km S of Manzanillo de Talamanca, E of Quebrada Hone Wark, lower slopes to upper slopes and summit, this individual located far from nearest grove of cultivated cacao in primary forest and with every appearance of being indigenous, 9°37’00” N, 82°39’30” W, 40–190 m, 4 Nov 1984 (fr.), *Grayum et al. 4400* (CR, MO). **Puntarenas**: Corredores, Fila Bella Vista, 11 Aug 1979 (fr.), *Ocampo 2439* (CR); Golfito, distrito Golfito, Parque Nacional Piedras Blancas, bosque primario donde se establecieron parcelas permanentes de muestreo, 223 m, 8º39’21.26’’ N, 83º12’05.94’’ W, 4 Jan 2014 (fl.),. *Jiménez et.al. 1376* (USJ); Osa [Agua Buena], forested near the airfield about 4 miles W of Rincon de Osa, Osa Peninsula, 8°42’00” N, 83°30’36” W, 30 m, 4 Jun 1968–7 Jun 1968 (fr.), *Burger & R. Stolze 5505* (CR, MO); Osa, Sierpe, Aguabuena, Reserva Forestal Golfo Dulce, 3.5 km W of Rincón, 4-hectare permanent plot 1 km N of BOSCOSA station, 8°43’0” N 83°31’0” W, 350 m, 12 Feb 1992 (st.), *Thomsen 589* (CR); Osa, Sierpe, Aguabuena, Reserva Forestal Golfo Dulce, 3.5 km W of Rincón, 4-hectare permanent simple plot 1 km N of BOSCOSA station, 8°43’0” N 83°31’0” W, 350 m, 12 Apr 1992 (st.), *Thomsen 602* (CR); Parque Nacional Corcovado Sirena, Rio Claro Trail, 8°27’36” N 83°34’48” W, 1–50 m, 24 May 1989 (fl.), *Kernan & Phillips 1109A* (MO, USJ); Quepos, distrito Savegre, Dos Bocas, Finca La Rosa, 9°23’36,60” N, 83°54’53,28” W, 550 m, 1 Sep 2013 (fl., fr.), *Chinchilla 744* (CR, USJ); Garabito, Reserva Biológica Carara [ahora Parque Nacional Carara], Valle del Tárcoles, saddle between Cerros Quebrada Bonita and Montañas Jamaica, headwaters of Quebrada Bonita, and ridge to N, 9°46’ N, 84°34’ W, 420–585 m, 27 Jul 1995 (fr.), *Grayum et al. 10763* (MO); Buenos Aires, Potrero Grande, Cuesta Pita, bosque primario en finca privada, 497 m, 8°55’51,23’’ N, 83°4’4,26’’ W, 23 Apr 2020 (fl.fr), *Cedeño et al. 1708* (USJ). **San José**: Turrubares, Western part of Montañas Jamaica, ca. 3 km NE of Bijagual de Turrubares, Carara Reserve [Ahora Parque Nacional Carara], 9°45’30” N, 84°33’00” W, 500–600 m, 7 Aug 1985 (fl., fr.), *Grayum et al. 5863* (CR, MO); Puriscal, Zona Protectora La Cangreja [Ahora Parque Nacional La Cangreja], cercanías del Río Negro, creciendo en pendiente que cae a una quebrada, 9°41’50” N 84°23’30” W,

450 m, 20 Oct 1992 (fr.), *Jiménez & Morales 1138* (CR); Puriscal, Z.P. La Cangreja [Ahora Parque Nacional La Cangreja], Cerros de Puriscal, Santa Rosa de Puriscal, bosque primario en las faldas de Fila La Cangreja, 27 Aug 1992 (fr), 500 m, 9°41'24" N 84°22'48" W, *Morales 551* (CR, MO) (Fig. 1).

Especímenes de *Theobroma cacao* provenientes de plantaciones

COSTA RICA. **Alajuela**: Río Segundo, Finca José Ma. Árias, 10°0'10.72" N, 84°11'44.3" W, 11 Juan 1980 (st.), *Hernández s.n.* (CR93718); Barrio San José, 19 Apr 1994 (fl.), *Quirós s.n.* (USJ-52553). **Cartago**: Turrialba, IICA [ahora CATIE], 21 Dec 1950 (fr.), *J. León 2001* (CR, USJ [2 pliegos]); Turrialba, IICA [ahora CATIE], 26 Jun 1967 (fl.), *Córdoba 647* (USJ); Turrialba, I.I.C.A, Oct 1970, *Cerdas et al, 8117* (USJ [3 pliegos]). Turrialba, I.I.C.A, 27 Mar 1950, *León 1341* (USJ); CATIE, 3 Nov 1974 (st.), *Vaughan s.n.* (USJ-13659). **Guanacaste**: Nicoya, 1 Jun 1949, *López 2596* (CR); Nicoya, Pedernal, 100 m, 1 Jan 1954, *León 4273* (CR). **Limón:** Talamanca, Cahuita, Cocoa plantations 1 to 3 km N of Bribri, 9°38' N, 82°50' W, 20 m, 10 Sep 1978 (fl.), *Burger & Antonio 10967* (CR); Guácimo, Parque Nacional Tortuguero, Cuatro Esquinas, 400 m al E de la casa-estación, 10°30'36" N 083°30'00" W, 2 m, 28 Nov 1987 (fr.), *Robles 1379* (CR, MO); Siquirres, Germania, Oct 1964 (st.), *Víquez s.n* (USJ-69487); Talamanca, Bajo Coen, 9°31' N 083°0' W 145 m, 28 Aug 2012 (st.), *Sylvester 14* (USJ). **Heredia**: Sarapiquí, La Selva Biological Station, area around boat landing at Tobias's house, W landing, 10°25'53" N, 84°00'13" W, 100 m, 23 Apr 1981 (fl.), *Folsom 9836* (MO); Sarapiquí, Finca La Selva, the OTS field station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 10°25'53" N, 84°00'13" W-10°25'53" N, 84°00'13" W, 100 m, 4 Oct 1980 (fl.), *Hammel 10039* (MO); Puerto Viejo de Sarapiqui, Finca La Selva, SE edge of air-conditioned lab clearing, 10°25'48" N, 084°00'00" W, 100 m, 21 Jun 1979 (fl.), *Sperry 514* (MO); Sarapiquí, La Selva Biological Station, 10°25'53" N, 84°00'13" W, 100 m, 5 Aug 1978 (fl.), *Grayum 1506* (MO); La Selva Biological Station, Sendero Surá 70 m der. 1 m, 10°25'53" N, 84°00'13" W , 100 m, 5 Dec 2006 (fl.), *Vargas 1566* (MO); Sarapiquí, La Virgen, La Tirimbina, 220 m, 3 Feb 1989 (fr), *Hunter 673* (CR); Sarapiquí, La Virgen, La Tirimbina, 220 m, 3 Feb 1989 (fr), *Hunter 680* (CR); Sarapiquí, La Virgen, La Tirimbina, 220 m, 3 Feb. 1989 (fr), *Hunter 699* (CR). **Puntarenas**: Punta Burica, creciendo en zona aledaña a río en posición de indígenas Guaymíes, 8 Mar 1979 (fr.), *Ocampo 2546* (CR); Golfito, Puerto Jiménez y alrededores, 14 Apr 1930, *Brenes 12334* (CR); Golfito, Puerto Jiménez, R.F. Golfo Dulce, Península de Osa, cultivado alrededores de Estación Agujas, 8°32' N, 83°25' W, 300 m, 24 May 2000 (fr.), *Acosta et al. 1458* (CR); Buenos Aires, Changena, Reserva Indígena Guaymí, 8°50'1" N, 83°5'27" W, 700 m, 11 Junio 2002 (fr.), *Frances 1* (CR); Buenos Aires, Changena, Las Vegas de Limoncito, 8°50'59" N, 83°5'75" W, 700 m,26 Octubre 2002 (fr), *Frances 28* (CR); Puntarenas, Wafer Bay, Isla del Coco, 23 Jan 2002 (fr.), *Trusty & Kesler 228* (CR); Volcán de Buenos Aires, 13 Feb 1968 (st.), *Villa* 20 (USJ). **San José**: Puriscal, Z.P. La Cangreja [Ahora Parque Nacional La Cangreja], Santa Rosa de Puriscal, creciendo en plantaciones abandonadas bajo el dosel del bosque, 9°41'24" N, 84°23'24" W, 400 m, 8 Dec 1992 (fr.), *Morales 359* (CR); Puriscal, La Cangreja [Parque Nacional La Cangreja], Santa Rosa, 400 m, 2 Feb 1973 (fr.), *Poveda 479* (CR, USJ); Puriscal, Chires, P.N. La Cangreja, Alto Concepción, Quebrada Grande, Sendero a Río Negro, 9°42'20" N, 84°21'55" W 500 m, 14 Sep 2003 (fl., fr.), *Morales & González 9878* (CR). (Fig. 1).

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POLYPOGON VIRIDIS (POACEAE): NEW TO LOUISIANA

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ABSTRACT

Polypogon viridis (Gouan) Breistr. is documented as growing outside of cultivation in Caddo Parish, Louisiana, the first record for the state. It is abundant in colonies in a city park in Shreveport.

We discovered *Polypogon viridis* (Gouan) Breistr., commonly known as water beardgrass or water bentgrass, growing in Columbia Park, a 4-hectare, frequently mowed, public park in Shreveport, Louisiana (Figs. 1, 2). This is the first record for this species in the state (Allen et al. 2004).

Voucher. **Louisiana**. Caddo Parish. City of Shreveport, Columbia Park (S of Columbia St., between Creswell Ave. and Line Ave., shaded mesic habitat near an intermittent stream, 2 May 2020, *M. & B. MacRoberts 8999*, 9000 (LSU, LSUS).

There are several stands of *Polypogon viridis* along the stream in Columbia Park, consisting of hundreds of individuals. The largest stand measures approximately 2 by 4 meters (Fig. 1). The plants are perennial, with culms sometimes decumbent and rooting at the lower nodes, which apparently accounts for the colonial tendency. Associated trees include *Betula nigra*, *Pinus taeda*, and *Pinus echinata*. Associated herbaceous species include *Alternanthera philoxeroides*, *Eleocharis tortilis*, *Hydrocotyle verticillata*, *Juncus bufonius,* and *Tradescantia ohiensis*.

Polypogon viridis is native to Europe and occurs as far west as Pakistan (Barkworth 2007). It is naturalized and established in the western USA east to Texas and Oklahoma (Kartesz 2014; Turner et al. 2003). Records from the Atlantic coast of the USA are based on plants found only on ballast dumps (Barkworth 2007). According to Nesom (2009), in Texas the species is not considered to be of particular threat to native species.

Interestingly, while researching this species we discovered a specimen collected by A.B. Langlois (Ewan 2005) in 1885 in Plaquemines Parish, Louisiana, at the mouth of the Mississippi River "on ballast ground" (Fig. 3). This specimen is now housed in WIS, making our discovery in Shreveport actually the second for the state.

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Figure 1. *Polypogon viridis*. Naturalized population in Columbia Park, Shreveport. 2 May 2020.

Figure 2. *Polypogon viridis*. Columbia Park, Shreveport. 2 May 2020.

Figure 3. *Polypogon viridis*. Louisiana. Plaquemines Parish. Port Eads, ballast ground, 6 May 1885, *Langlois s.n.* (WIS).

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ADDITIONS TO THE VASCULAR FLORA OF CADDO PARISH, LOUISIANA

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ABSTRACT

The vascular flora of Caddo Parish is updated. Field research has yielded four new species to the area: *Alternanthera sessilis*, *Plantago major*, *Polycarpon tetraphyllum*, and *Polypogon viridis*.

Since the publication of our "An updated annotated vascular flora of Caddo Parish, Louisiana, with notes on regional phytogeography and ecology" (MacRoberts & MacRoberts 2006) and several updates recording new species to the Parish (Kelley 2019; MacRoberts & MacRoberts 2017, 2020; MacRoberts et al. 2018), we have continued to locate interesting additions. All of the species reported here were found in Columbia Park, a 4-hectare, frequently mowed and highly disturbed public park in Shreveport, Louisiana (see brief description in MacRoberts et al. 2020). All of the species reported here as new to Caddo Parish are non-native. According to Nesom (2009), in Texas these species are not considered to be a threat to native species. The Caddo Parish vascular plant list now stands at 1451 species, of which 17% are non-native.

AMARANTHACEAE

Alternanthera sessilis (L.) R. Br. ex DC. *MacRoberts & MacRoberts 9011, 9012* (LSUS, LSU).

This species was found on August 12 and 13 in two wet areas near a stream. Associated species include *Alternanthera philoxeroides*, *Calyptocarpus vialis*, *Diodia virginiana*, and *Paspalum pubiflorum*.

CARYOPHYLLACEAE

Polycarpon tetraphyllum (L.) L. *MacRoberts & MacRoberts 9004, 9005* (LSUS, LSU).

On 8 June 2020, we discovered *Polycarpon tetraphyllum* (L.) L., commonly known as four-leaf manyseed, growing in shaded dry soil. This is the second Louisiana record for this native of Europe and the Mediterranean (Allen et al. 2010). There were many clusters of this species over a half hectare of relatively flat, highly compacted ground (Figs. 1 and 2). Associated species included *Pinus taeda, Cynodon dactylon, Digitaria ciliaris, Digitaria ischaemum, Prunella vulgaris, Salvia lyrata, Sida spinosa, Stenotaphyrum secundatum,* and *Trifolium repens*.

PLATAGINACEAE

Plantago major L. *MacRoberts & MacRoberts 9008* (LSUS, LSU)

While widely scattered throughout the USA (Kartesz 2014), this native of Europe has apparently not been reported for Caddo Parish (MacRoberts & MacRoberts 2006). We found three plants on 14 July 2020, growing is a wet area near a small stream dominated by *Acmella oppositifolia, Colocasia esculenta*, and *Phyllanthus urinaria*.

POACEAE

Polypogon viridis (Gouan) Breister.

New to both Louisiana and Caddo Parish, discussed in a previous paper (MacRoberts et al. 2020).

Figure 1. *Polycarpon tetraphyllum* habitat in Columbia Park, Shreveport.

Figure 2. *Polycarpon tetraphyllum* in Columbia Park, Shreveport.

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Guy Nesom confirmed our initial identification of *Polycarpon tetraphyllum*. M. Jerome Lewis aided with the figures. Jennifer Kluse aided with the identification of *Alternanthera sessilis*.

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NUEVO REGISTRO DE *EHRHARTA* (POACEAE) EN LA CIUDAD DE MÉXICO, MÉXICO

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RESUMEN

Ehrharta erecta var. *erecta* es una gramínea invasora, recientemente reportada como introducida en México, en los estados de Baja California y Michoacán. Se registra por primera vez esta taxón en la Ciudad de México. Se proporcionan una descripción, ilustraciones, y un mapa con la distribución geográfica conocida en la ciudad.

ABSTRACT

Ehrharta erecta var. *erecta* is an invasive grass recently recorded as introduced in Mexico in the states of Baja California and Michoacan. This taxon is documented here for the first time in Mexico City. A description, illustrations, and a map with the known geographical distribution in the city are provided.

El género *Ehrharta* Thunb. (Poaceae: Oryzoideae: Ehrharteae) incluye aproximadamente 25 especies a nivel mundial (Soreng et al. 2017), la mayoría de ellas distribuidas en Sudáfrica y unas pocas de Indonesia a Nueva Zelanda (Clayton & Renvoize 1986). Tres especies sudafricanas se encuentran establecidas en los Estados Unidos de América (Barkworth 2007) y una de ellas, *Ehrharta erecta* Lam., recientemente se registró por primera vez en México, en los estados de Baja California y Michoacán (Sánchez-Ken 2019). La especie es considerada como invasora, capaz de colonizar múltiples hábitats (Ray et al. 2018). Se reconocen tres variedades (var. *erecta*, var. *abyssinica* Pilg., y var. *natalensis* Stapf.), las cuales se distinguen por el tamaño de las espiguillas y la textura de la segunda lema estéril (Sánchez-Ken 2019). Durante un recorrido reciente en la Ciudad de México, se detectaron numerosos individuos de la variedad típica creciendo como malezas.

EHRHARTA ERECTA Lam., Encycl. 2(1): 347. 1786. **TIPO: SUDÁFRICA.** Cabo, *M. Sonnerat s.n.* (holotipo: P).

Plantas herbáceas, perennes, cespitosas; **tallos** decumbentes a erectos, 0.3–1 m de largo, 1.5–3 mm de ancho, ramificados hacia la base, nudos glabros, los inferiores en ocasiones enraizando, entrenudos glabros; **vainas foliares** más cortas que los entrenudos, márgenes libres, glabras, con aurículas apicales, frecuentemente ciliadas; **lígulas** hasta 3 mm de largo, glabras, laceradas con la edad; **láminas foliares** 5–15 cm de largo, 2–15 mm de ancho, lineares, aplanadas, glabras; **inflorescencias** 5–20 cm de largo, terminales, en forma de panículas contraídas a extendidas, erectas a péndulas; **espiguillas** 3.4–3.8 mm de largo, elipsoides, comprimidas lateralmente, con 3 flósculos, los 2 inferiores estériles y sin páleas, el terminal bisexual; **desarticulación** por arriba de las glumas, los flósculos cayendo unidos; **pedicelos** más cortos a más largos que las espiguillas, escabrosos; **glumas** 2, más cortas que los flósculos, desiguales, elipsoides, ápice agudo, escabriúsculas hacia el ápice, la inferior 1–2 mm de largo, con 3–5 nervaduras, la superior 2–2.5 mm de largo, con 5 nervaduras; **lemas inferiores** desiguales, elipsoides, aquilladas, ápice truncado, cartáceas, glabras o esparcidamente escabriúsculas, la primera 3–3.2 mm de largo, lisa, con un callo basal, la segunda 3.3–3.5 mm de largo, rugosa transversalmente hacia el ápice, con un par de aurículas basales; **lema terminal** 3–3.3 mm de largo, ovada, aquillada, ápice obtuso, cartácea, glabra, con 5–7 nervaduras tenues; **pálea terminal** casi

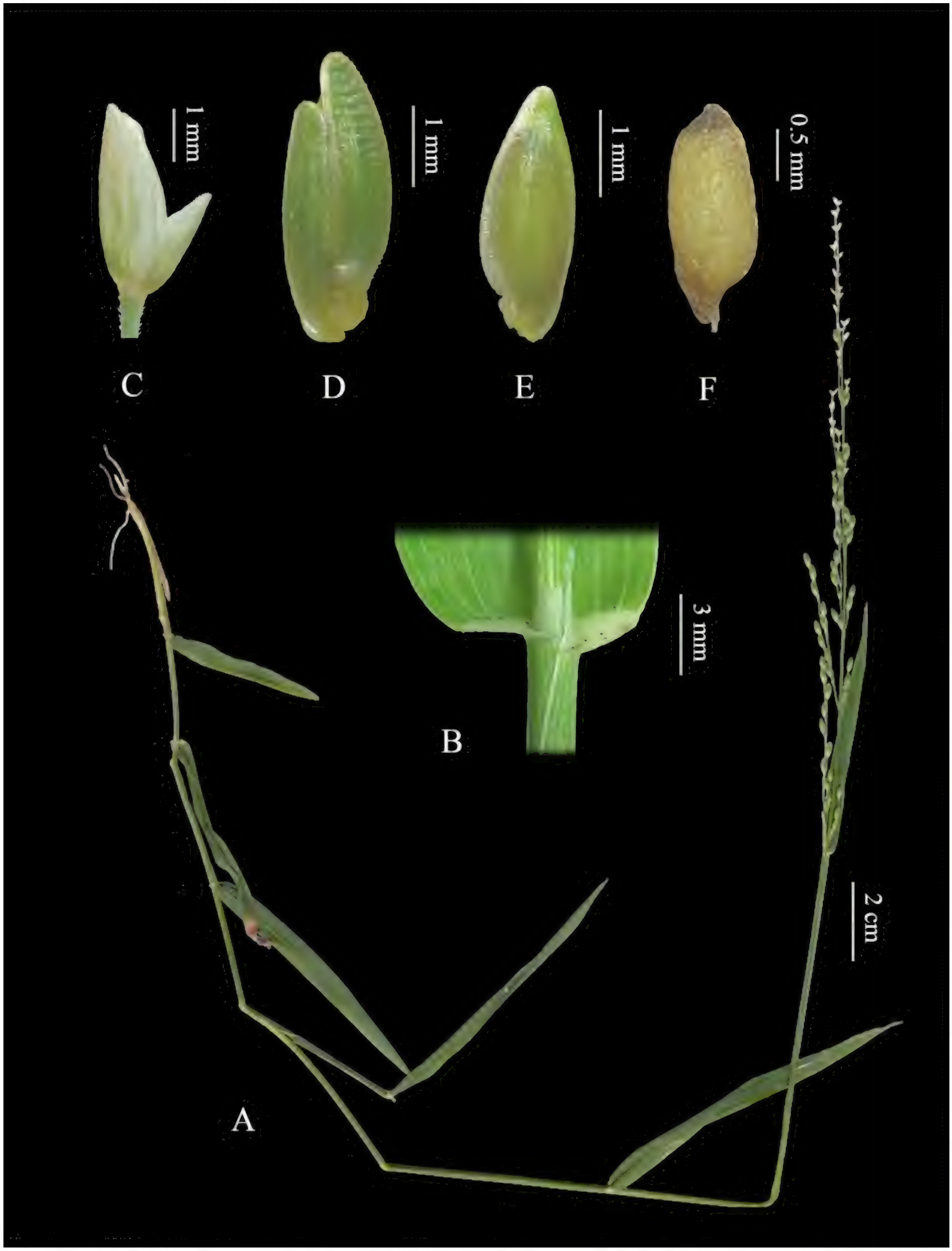

Figura 1. *Ehrharta erecta* var. *erecta*. A. Hábito. B. Detalle del ápice de la vaina, mostrando las aurículas y la lígula. C. Glumas. D. Flósculos. E. Flósculo terminal. F. Cariópside. Basado en *Vigosa-Mercado 110* (MEXU).

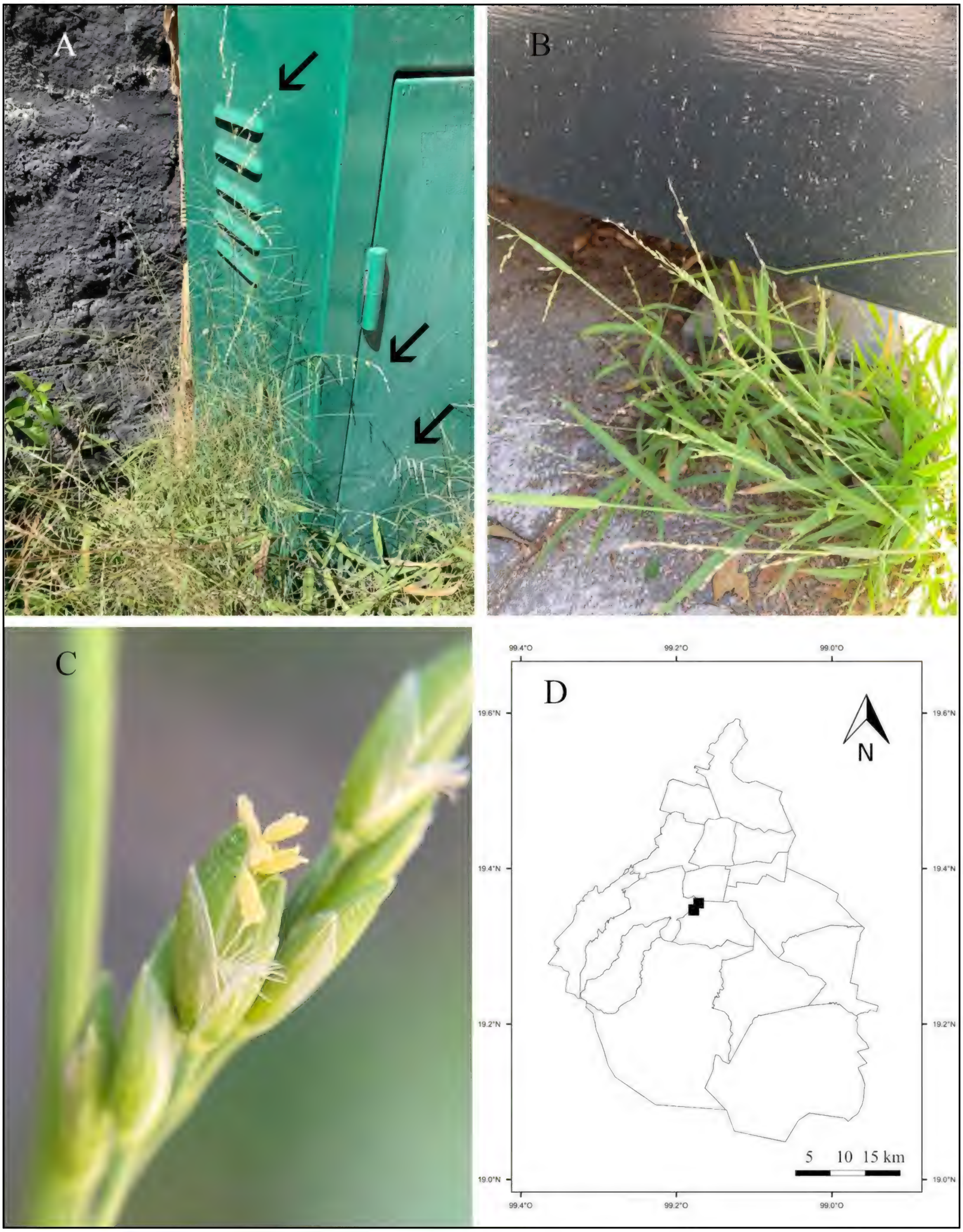

Figura 2. A-B. Individuos de *Ehrharta erecta* var. *erecta* in situ. C. Espiguilla en antesis, mostrando cinco de las seis anteras y un estigma plumoso. D. Distribución geográfica conocida en la Ciudad de México.

tan larga como la lema, ovada, aquillada, cartácea, escabríscula en la quilla, nervaduras no evidentes; **raquilla** cortamente prolongada más allá de la base del flósculo terminal; **lodículas** 2, libres; **anteras** 6, 0.8–1.5 mm de largo; **ovario** glabro, estilos 2, plumosos; **frutos** 2–2.4 mm de largo, en forma de cariópsides, elipsoides, comprimidos lateralmente, con una pequeña proyección en la base (Figs. 1, 2).

Ejemplares examinados. MÉXICO. Ciudad de México. Coyoacán: Esquina de Cerrada de Salvador Novo con Calle Salvador Novo, ca. 200 m de la Calle Francisco Sosa hacia Avenida Miguel Ángel de Quevedo, 19.34738° N, 99.17758° O, 4 Oct 2020, *Vigosa-Mercado 109* (MEXU); esquina de Calle Salvador Novo con Avenida Miguel Ángel de Quevedo, 19.34641° N, 99.17785° O, 4 Oct 2020, *Vigosa-Mercado 110* (MEXU); Viveros de Coyoacán, Calle Celtis, entre las Calles Catalpas y Fresnos, 19.35554° N, 99.17144° O, 4 Oct 2020, *Vigosa-Mercado 111* (MEXU).

Comentarios. Este taxón no ha sido registrado anteriormente en los trabajos florísticos del centro de México (p. ej., Herrera-Arrieta & Rzedowski 2001). Probablemente la distribución geográfica de este taxón sea más amplia de lo que sugieren las colecciones biológicas, o bien, puede incrementarse en la ausencia de un control de malezas. Sánchez-Ken (2019) sugirió que probablemente las cariópsides provinieron de los Estados Unidos de América, en el cargamento de ferrocarriles o adheridas a personas o animales. Esta hipótesis podría también explicar la presencia del taxón en la Ciudad de México. En cuanto a su estatus de taxón invasor, Ray et al. (2018) mencionaron que aparentemente no representa una amenaza significativa a especies nativas de flora, al menos a corto plazo.

Finalmente, Lamarck (1786) mencionó en el protólogo de la especie, que el ejemplar examinado por él le fue enviado por M. Sonnerat y no se encontraba etiquetado, por lo que no se sabe si el ejemplar provino de Cabo (Sudáfrica) o la India. Al respecto, Sánchez-Ken (2019) indicó que el holotipo probablemente fue colectado en Sudáfrica y corresponde a un ejemplar depositado en el herbario histórico de Lamarck en París.

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THREE SPECIES OF GREENHOUSE OR CONTAINER NURSERY WEEDS VERIFIED OR NEW TO KENTUCKY

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ABSTRACT

Recent collections of greenhouse and container nursery weeds have resulted in three species verified or new to Kentucky: *Acalypha arvensis*, *Amaranthus blitum*, and *Parietaria floridana*.

ACALYPHA ARVENSIS Poep. & Endl. [Euphorbiaceae]

Voucher specimen. KENTUCKY. Madison Co: Richmond, Eastern Kentucky University greenhouses, several plants in pots with tropical foliage or under benches, 4 Oct 2019, *Adanick 586* (EKY).

This is the first report of *Acalypha arvensis* from Kentucky (Figure 1) and the first outside of Florida (Levin 2016) and Mobile Co., Alabama (Keener et al. 2019), where it was found near a commercial plant nursery and florist (*Horne 3288*, UWAL). Field copperleaf is a neotropical plant native to Central America, Mexico, and the West Indies. It was first documented in the 1980s at the Mission Road greenhouse of Florida State University (*Anderson 13476*, FSU) and became established through the disposal of growing media (G.A. Levin, pers. comm.). Although it is scattered in eight Florida counties (Wunderlin et at. 2020), there is no evidence that field copperleaf has escaped to establish itself outside of greenhouses in Kentucky.

AMARANTHUS BLITUM L. [Amaranthaceae]

Voucher specimens. KENTUCKY. Barren Co.: Glasgow, Shipley's Greenleaf Nursery, 2918 Scottsville Road, large plant under bench in large greenhouse nearest to Hwy 31E, 26 Sep 2019, *Adanick 587* (APSC). Boone Co.: Burlington, Ammon Nursery, Camp Ernst Road, in back of storage building near mulch bins, 3 Oct 2019, *Adanick 588* (APSC). Fayette Co.: Lexington, Michler's Florist and Greenhouse, in walkway near receiving area for tropical foliage shipments, 17 Jun 2019, *Adanick 577* (EKY); Lexington Sunshine Grow Shop, Southland Drive, few plants under outdoor display benches, 17 Jun 2019, *Adanick 578* (EKY). Madison Co.: Richmond, Eastern Kentucky University greenhouses, many growing in walkways and under benches, high rate of germination, 21 Sep 2018, *Adanick 425* (EKY), *Adanick 585* (APSC). Nelson Co.: Bardstown, MVP Garden Center, 5729 New Haven Road, many in walkways and under benches, [employees verified import of this weed by tropical plants from Florida], 16 Jul 2020, *Adanick 20.115* (APSC). Rowan Co.: Morehead, Morehead State University (MSU) Greenhouses, Greenhouse #4, many growing in walkways and under benches, 24 Jun 2019, *Adanick 564* (EKY); MSU Greenhouse #2, many growing in walkways and under benches, 24 Jun 2019, *Adanick 540* (EKY); MSU Greenhouse #1, many growing in walkways and under benches, 24 Jun 2019, *Adanick 510* (APSC); MSU Greenhouse #5, many growing in walkways and under benches, 24 Jun 2019, *Adanick 548* (APSC). Warren Co.: Bowling Green, Hillview Garden and Florist, 2209 Nashville Road, 7-8 plants in walkways in container nursery/display gardens, 16 Jul 2020, *Adanick 20.116* (APSC).

This is the first report of *Amaranthus blitum* from Kentucky (Figure 2). Purple amaranth is a pantropical weed sporadically found in greenhouses, nurseries, ornamental gardens, horticultural plantings, and ruderal habitats in Africa, Eurasia, Central America, South America, and the USA (Mosyakin & Robertson 2003). In the southern and northeastern USA, its distribution range is New Hampshire southward through the Atlantic coastal states to Florida and the Midwest in Arkansas, Louisiana, Missouri, Ohio, Tennessee, and Texas, and to the west in California, Utah, and Washington (USDA, NRCS 2020). In Kentucky, it has been verified in nine counties (Barren, Boone, Campbell, Fayette, Jessamine, Madison, Nelson, Rowan and Warren) to date. It has also been confirmed by the first author that populations are becoming established outdoors (Jessamine and Madison counties).

Purple amaranth was first found in the northeastern USA from a collection in New York's Central Park in 1861 (Costea et al. 2001; Costea & Tardiff 2003) and was collected in 1877 from ship's ballast in Philadelphia, Pennsylvania (Burk 1877), and at Camden, New Jersey, in 1879 (*Parker s.n.*, CHRB). It has since spread widely, presumably through the horticultural trade. Nursery workers in Nelson County and a greenhouse owner in Jessamine County suggest this weed is being introduced from tropical plants purchased from Florida (P. Cooper, pers. comm.).

If infraspecies are warranted, our specimens are probably referable to *Amaranthus blitum* subsp. *emarginatus* (Moq. ex Uline & Bray) Carretero, Muñoz, Garmendia, & Pedrol, from Costea and Tardiff (2003).

PARIETARIA FLORIDANA Nutt. [Urticaceae]

Voucher specimen. KENTUCKY. Madison Co: Richmond, Eastern Kentucky University greenhouse ('Poly-house') in aisleways to moist area near ground beds, basal divergence of main lateral leaf veins; achenes measure 0.74 mm long with flanged stipe, 29 Feb 2020, *Adanick 20.100* (EKY).

This is the first verified report from Kentucky (Figure 3). Although first found only inside greenhouses, several plants were found in July of 2020 established outdoors at a greenhouse facility in Jessamine County by the first author (*Adanick 20.118*, APSC).

A previous report of this species from Carter, Pulaski, and Wayne counties (Braun 1943) was based on misidentified specimens (*Braun 2269, 3098, 4371,* US) of *Parietaria pennsylvanica* Muhl. ex Willd. A diminutive Kentucky specimen from a sandstone rock house in Menifee County (*Taylor, s.n.*, BEREA), annotated as *P. floridana* is so completely glued to the herbarium sheet that fruit and achene morphology cannot be observed. A similar specimen from a comparable sandstone cliff habitat in Powell County was collected during the summer of 2020 (*Adanick 20.121*, APSC) and grown to maturity by the first author.

Subsequent comparisons of seed morphology and venation and examination of related herbarium specimens (*Medley 7142-82*, APSC; *Leonard 7178*, NCU; *Fields 820*, EKY; *Stuart Lassiter 2977*, TENN) suggest the Taylor specimen and the Powell County specimen may be ecological variants of *Parietaria pensylvanica*, as neither specimen exhibits basal divergence of the leaf veins or the flanged stipe of the achene (Hinton 1968). Further study is warranted.

Parietaria floridana is otherwise known from New Hampshire and Maryland, south to Florida and west to Arkansas and Texas (USDA, NRCS, 2020). Florida pellitory is native to North America and occurs mostly on the outer Coastal Plain (Weakley 2015).

Figure 1. *Acalypha arvensis* from a greenhouse in Madison Co., Kentucky (*Adanick 586*, EKY).

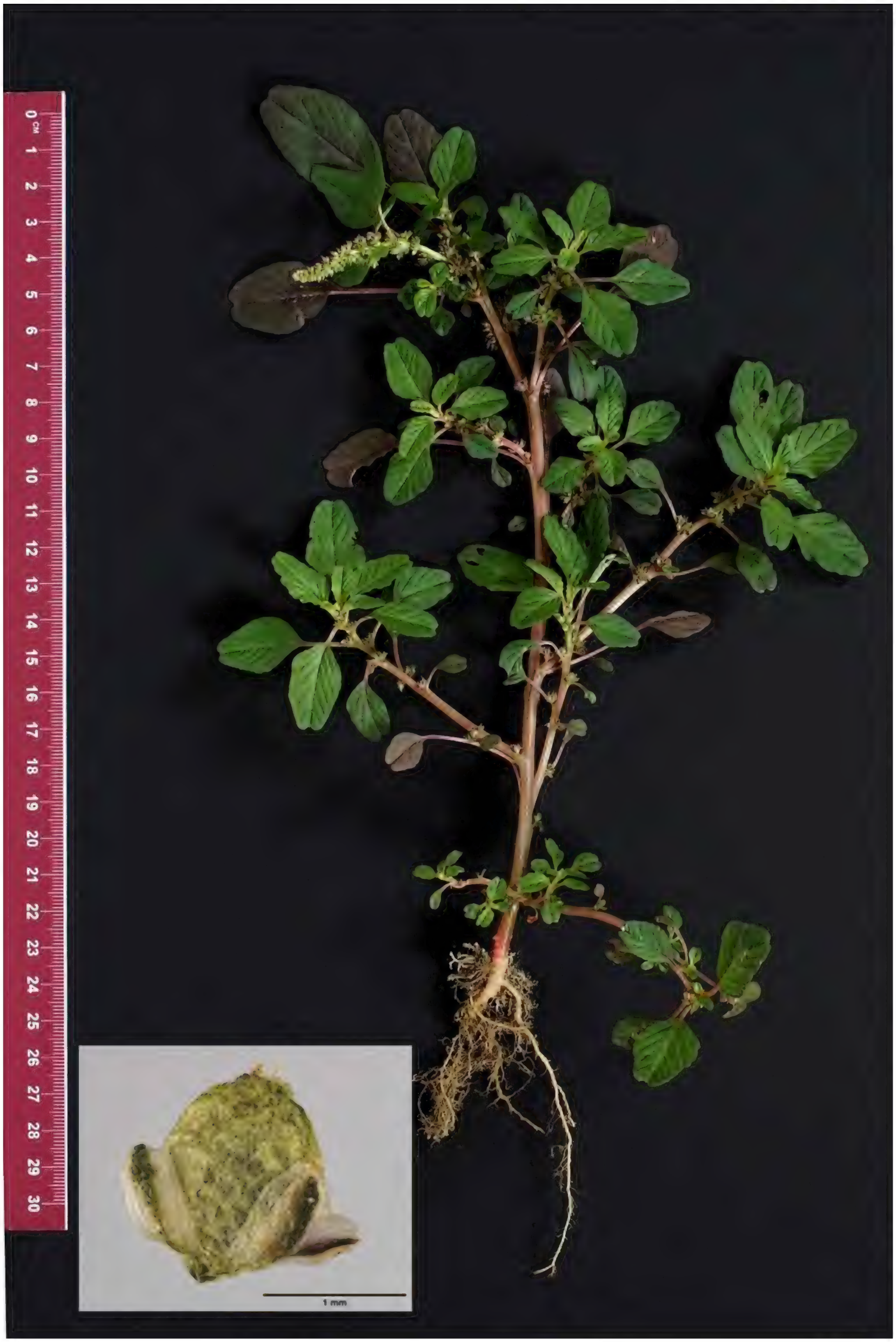

Figure 2. *Amaranthus blitum* from a greenhouse in Jessamine Co., Kentucky (*Adanick 576*, EKY). Inset: fruit with 3 tepals.

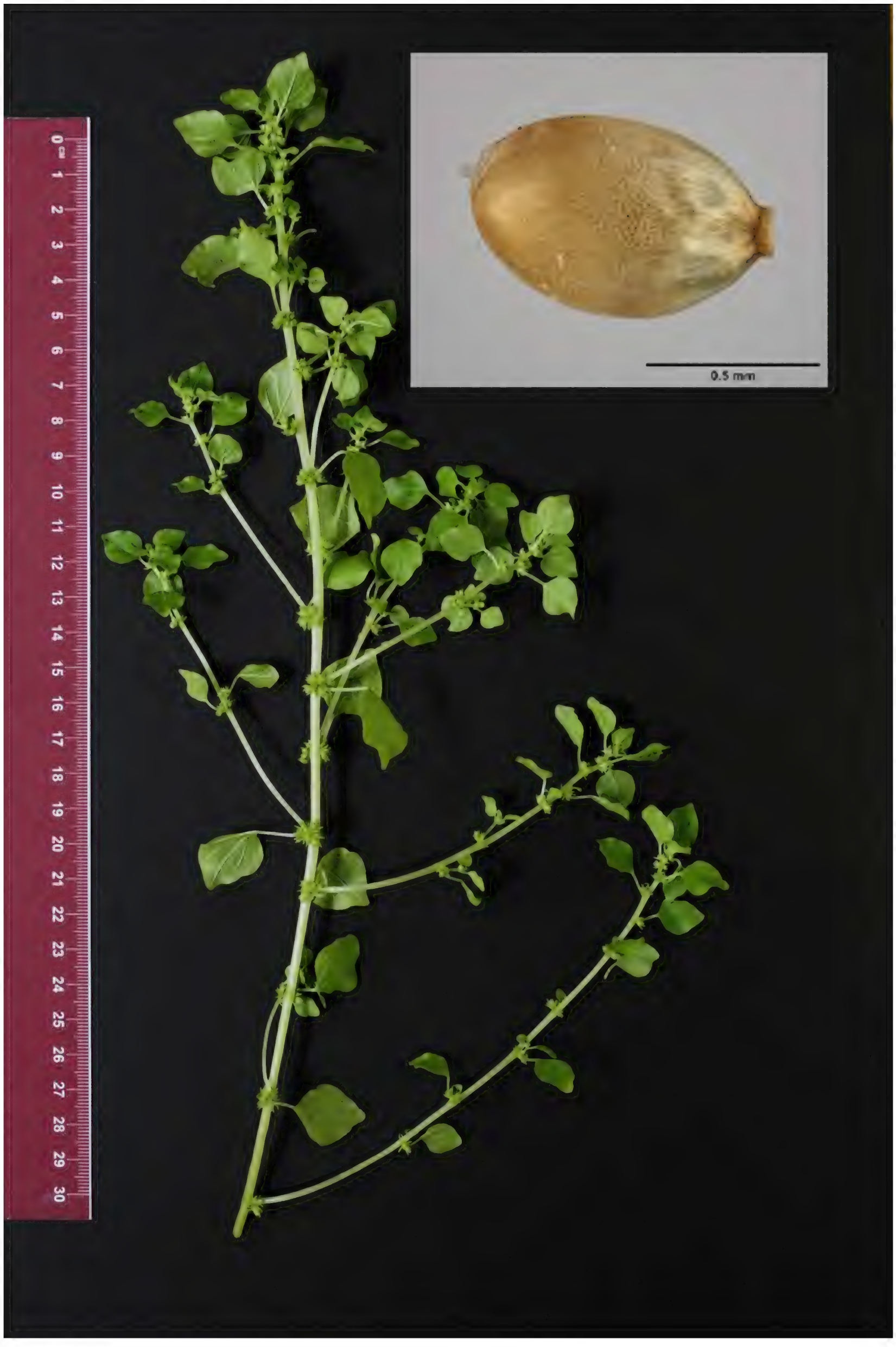

Figure 3. *Parietaria floridana* from a greenhouse in Madison Co., Kentucky (*Adanick 20.100*, EKY). Inset: achene with flanged stipe.

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NEW SPECIES OF MONKEYFLOWER (*ERYTHRANTHE*: PHRYMACEAE) FROM THE CALIFORNIA SIERRA

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ABSTRACT

Two new species of *Erythranthe* are recognized, both apparently narrowly endemic to Inyo County in the Sierra Nevada of central California and both members of sect. *Simiolus*. Both are annuals with autogamous flowers and hypothesized to be closely related to *E. nasuta*. **Erythranthe bergeri** Nesom, **sp. nov.**, has distal leaves that are connate-perfoliate with upturned margins. **Erythranthe angulosa** M. Berger, **sp. nov.**, produces swollen axillary organs at bases of stem and peduncles — these organs attract ants and perhaps are extrafloral nectaries. In situ photos document both species.

Field exploration by Berger in northern Inyo County, California, has discovered two highly distinctive species of *Erythranthe*. Both are previously undescribed members of sect. *Simiolus*.

ERYTHRANTHE BERGERI Nesom, **sp. nov. TYPE**: **California**. Inyo Co.: 3.2 air mi NW of center of Big Pine, WSW of Warren Lake, just S of County Road, 37.190678 -118.342133, cracks and fissures in granite outcrop near mouth of large, seasonally wet wash, 4060 ft, 10 May 2020, *M. Berger s.n.* (holotype: RSA; isotype: UC).

Similar to *Erythranthe nasuta* in its annual duration, 4-angled stems, slightly elongate upper calyx lobe, and plesiogamous (and presumably autogamous) flowers but different in its evenly and densely hirtellous vestiture (stems, leaves, calyx), connate-perfoliate distal leaves, the distalmost pairs forming cuplike structures with upturned margins, leaf margins shallowly and irregularly dentate-serrate, and its calyces with raised-thickened ridges and membranous inter-ridge areas.

Annual, taprooted. **Stems** erect to ascending-erect or decumbent, ca. 25–50 cm, 4-angled, simple or branched from proximal nodes, evenly and densely hirtellous, eglandular. **Leaves** basal and cauline, proximal to medial petiolate, distal medial to distal abruptly becoming epetiolate and connate-perfoliate, petioles 4–10 cm long, blades (proximal to medial) broadly ovate to elliptic-ovate or suborbicular, 3–6.5 cm long, palmately 5–7-nerved, proximal largest, apices acute to obtuse or rounded, bases (proximal and lower cauline) cuneate to truncate or subcordate, margins shallowly and irregularly dentate to dentate-serrate or nearly lacerate-dentate, commonly doubly toothed, green on both surfaces or sometimes purplish abaxially, densely and evenly hirtellous on both surfaces with dull, terete, sharp-pointed, nonglandular hairs, eglandular. **Flowers** usually from distal nodes but sometimes from medial to distal, 2 per node; flowering branches from proximal to medial nodes. **Fruiting pedicels** 10–20 mm, densely hirtellous, eglandular. **Fruiting calyces** densely and evenly hirtellous, eglandular, 11–15 mm long, green and without red or purple markings, ridges raised and thickened, inter-ridge areas membranous and transparent, lobes closing, upper lobe often slightly elongate. **Corollas** yellow, sometimes with a sparsely red-spotted tube-throat base, without red marking on the lower lip, tube-throat cylindric, 6–10 mm, exserted 2–4 mm beyond calyx margin, limb weakly bilabiate, expanded ca. 2–3 mm (pressed). **Plesiogamous**; anther pairs and stigma at the same level. Figures 1-7.

Known only from the type collection.

The only other species of *Erythranthe* with connate-perfoliate leaves is *E. glaucescens* (Fig. 10), which is restricted to Butte and Tehama counties (California) and is characterized by broadly bilabiate, herkogamous-allogamous flowers and glabrous-glaucous vestiture (Fig. 8). Given the otherwise wide morphological disparity between *E. bergeri* and *E. glaucescens*, the unique foliar feature probably developed in parallel. *Erythranthe glaucescens* is hypothesized to be closely related to *E. nudata*, *E. percaulis*, and *E. filicifolia* (Nesom 2019).

Erythranthe bergeri has more in common with *E. nasuta* (Figs. 11-14), *E. laciniata*, and *E. pardalis* (subgroup E of the "Guttata group" in Nesom 2019). These plants are annual in duration with flowers often produced at all nodes (proximal to distal). Flowers of *E. nasuta* often are reduced in size and autogamous, like those of *E. bergeri*. *Erythranthe nasuta* is variable and broadly distributed through the western USA; *E. laciniata* and *E. pardalis* are California endemics with relatively narrow ranges. Subgroup E is expanded here to include the two new species described in this manuscript as well as the widely distributed *E. microphylla*, which also has 4-angled stems.

Among the species of subgroup E, the closest evolutionary relative of *Erythranthe bergeri* is hypothesized here to be *E. nasuta*, emphasizing their 4-angled stems and overlap in vestiture. *Erythranthe nasuta* does not produce the pervasively hirtellous vestiture characteristic of *E. bergeri* but the adaxial leaf surfaces usually are hirtellous and stems and calyces are variably so (between populations). Hirtellous vestiture also is produced by *E. microphylla* and especially variants of *E. guttata* sensu stricto.

Figure 1. Locality of *Erythranthe bergeri*. Cracks and fissures of granite outcrop near mouth of large, seasonally wet wash, northwest of Big Pine, Inyo County. Google Earth and Google Maps.

Figure 2. *Erythranthe bergeri*. Habitat on faces of broad granite fissure at the type locality. Photo by Matt Berger, 10 May 2020.

Figure 3. *Erythranthe bergeri*. Cluster of plants from narrow crevice in granite, showing the distinction/transition from proximal, petiolate leaves to distal, perfoliate ones. Photo by Matt Berger.

Figure 4. *Erythranthe bergeri*. Isotype (UC).

Figure 5. *Erythranthe bergeri*. Inflorescences and upper cauline leaves, showing the cuplike structures formed by distal connate-perfoliate leaves. Details from Figure 3.

Figure 6. *Erythranthe bergeri*. Top: Upper midcauline leaves. Bottom: lower midcauline leaves, with depauperate branches and flowers from axils, connate-perfoliate by petiole-like base. Photos by Matt Berger.

Figure 7. *Erythranthe bergeri*. Inflorescence of mostly post-anthesis flowers, showing calyces with raised-thickened angles and membranous-transparent inter-ridge areas. Detail from Figure 3.

Figure 8. *Erythranthe bergeri*. Calyx and corolla. Photo by Matt Berger. Photos in Figs. 6 and 9 show corollas with a broader tube-throat and faint red markings on its base.

Figure 9. *Erythranthe bergeri*. Corolla and mature calyx. Photos by Matt Berger.

Figure 10. *Erythranthe glaucescens*, Butte County, California, May 2018. Photo by Evan D. MacKinnon, from CalPhotos. The connate-perfoliate leaves probably developed independently of those of *E. bergeri*.

Figure 11. *Erythranthe nasuta*, Wheeler Co., Oregon. *Stiles 00-02* (WTU).

Figure 12. *Erythranthe nasuta*, El Dorado Co., California, May 2019. Photo by Mark Egger, Flickr, by permission.

Figure 13. *Erythranthe nasuta*, Fresno Co., California, June 2017. Photo by Mark Egger, Flickr, by permission. Distal leaves are epetiolate with bases contiguous but not connate.

Figure 14. *Erythranthe nasuta*. Top and middle: Monterey Co., California, April 2019. Bottom: El Dorado Co., California, May 2019. Photos by Mark Egger, Flickr, by permission. Variation in flower morphology.

ERYTHRANTHE ANGULOSA M. Berger, **sp. nov.** **TYPE**: **California**. Inyo Co.: SW of Lone Pine, Horseshoe Meadows Road, 2.5 road mi ENE of Last Chance Meadow Research Natural Area and area of campgrounds and trailheads, 36.467044 -118.134064, granite cliffs and rock faces on N side of road, 9580 ft, 17 Jul 2020, *M. Berger s.n.* (holotype: RSA).

Similar to *Erythranthe nasuta* in its annual duration, 4-angled stems, tendency for stems and leaves to become purplish, and very small, plesiogamous (and presumably autogamous) flowers produced at all nodes (proximal to distal) — but distinct in its habit appressed against cliff faces, swollen axillary organs (at bases of stem and peduncles) that perhaps are extrafloral nectaries, completely glabrous stems, pedicels, and calyces, smaller calyces without a protruding upper lobe, and calyx lobes rolled nearly into cylinders..

Annual (probably), roots not seen. **Stems** decumbent, appressed against rock faces, ca 5–20 cm, sharply 4-angled, simple or branched from proximal nodes, glabrous, eglandular. **Leaves** basal and cauline or basal absent at flowering, sparsely hirtellous on both surfaces with dull, terete, sharp-pointed, eglandular hairs, more or less purplish on the lower surface or both surfaces, proximal to medial largest and persistent, petiolate, petioles 15–35 mm (absent distally), blades (of petiolate leaves) broadly ovate to subreniform, 20–45 mm wide, palmately 5-nerved, margins shallowly crenate to dentate, base truncate to subcordate, apex obtuse to acute, distal epetiolate with deltate blades with long-acute apices. **Swollen organs** produced at base of pedicels and stems at axils, appearing thin-walled and inflated, apparently exuding liquid drops. **Flowers** from basal to distal nodes, 2 per node; fruiting pedicels 10–25 mm, decreasing in length distally, glabrous, eglandular. **Fruiting calyces** mostly 7–9 mm long, nodding, glabrous, eglandular, often purple-spotted, lobes rolled nearly into cylinders with rounded apices, lower lobes curving upward and closing the mouth at maturity, upper lobe not prominently elongate. **Corollas** yellow, red-dotted along the palate ridges and with a red splotch at the base of the lower lip, tube-throats narrowly funnelform, exserted ca. 4–6 mm beyond calyx margin, limb bilabiate, expanded ca. 6 mm (pressed). Herkogamous; anther pairs and stigma at slightly separated levels.

Known only from the type collection.

The axillary organs of *Erythranthe angulosa* are unique in Phrymaceae. As they appear to be exuding liquid droplets (Fig. 23) and ants were observed on leaves and around the axillary organs (Figs. 23, 24), it is possible that they are extrafloral nectaries supporting a mutualistic interaction. On drying, these organs shrink to obscure but still perceptible swellings.

If these organs are extrafloral nectaries, the nature of possible benefit to plants of *E. angulosa* is obscure. Involvement of ants in floral biology is unlikely because the flowers show markings and morphology for bee pollination. *Erythanthe* seeds are minute and probably dispersed by wind and water rather than by insect mediation. Leaf herbivory in monkeyflowers occurs only rarely, but Figure 22 shows calyces and fruits eaten away and ants perhaps are involved with defense from predation. In situ observations are needed.

The species closest in morphology and those presumably most closely related to *Erythranthe angulosa* are *E. nasuta* (Figs. 11-14), *E. laciniata*, *E. pardalis*, and *E. microphylla* — subgroup E of the "Guttata group" (see comments above following *E. bergeri*; Nesom 2019). The present manuscript adds *E. bergeri* and E. *angulosa* to this subgroup and it is hypothesized here that these two with *E. nasuta* and *E. microphylla* form a clade characterized by 4-angled stems (probably an apomorphic feature) and hirtellous vestiture (probably plesiomorphic). Among the "subgroup E" species, even those with herkogamous flowers have small corollas with a slight degree of separation between anthers and stigma, and autogamy is common (Bodbyl Roels & Kelly 2011). *Erythranthe angulosa* differs from *E. nasuta* most conspicuously in its axillary organs and smaller calyces with subcylindric lobes.

Figure 15. Locality of *Erythranthe angulosa*. Top: Granite cliffs and faces at the type locality along Horseshoe Meadows Road. Bottom: Arrow points to the area of bare, exposed granite pictured in the upper photo. Google Earth.

Figure 16. *Erythranthe angulosa*. Habitat on granite cliff face at the type locality. Photo by Matt Berger, 17 Jul 2020.

Figure 17. *Erythranthe angulosa*. Corolla. Photo by Matt Berger.

Figure 18. *Erythranthe angulosa*. Stems and leaves more or less appressed against the rock face. Photo by Matt Berger.

Figure 19. *Erythranthe angulosa*. Inflorescence from same plant as in Figure 17. Photo by Matt Berger.

Figure 20. *Erythranthe angulosa*. Calyces after corollas shed. Photos by Matt Berger.

Figure 21. *Erythranthe angulosa*. Ant on green adaxial leaf surface. This branch comprises the holotype: Photo by Matt Berger.

Figure 22. *Erythranthe angulosa*. Fruit predation — calyces also partially eaten away.

Figure 23. *Erythranthe angulosa*. Swollen axillary organs at stem and peduncle bases. Arrows point to a small droplet apparently exuded from swollen organ. Photos by Matt Berger.

Figure 24. *Erythranthe angulosa*. Swollen axillary organs at stem and peduncle bases. Photo by Matt Berger.

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SOAPBERRY (*SAPINDUS* L.) IN ARIZONA

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ABSTRACT

Physical characteristics of western soapberry, *Sapindus saponaria* var. *drummondii*, are illustrated to facilitate their identification and conservation in Arizona. Larger thickets, composed of hundreds to thousands of tightly clustered trees, usually occur in riparian or riparian-adjacent areas, though soapberry trees and shrubs occur in a variety of habitats. We illustrate soapberry thickets using a combination of ground-based and aerial photography from three primary study sites in southern Arizona.

Soapberry trees and shrubs (*Sapindus* spp.) have a wide distribution (Figs. 1–2) and are important for indigenous peoples in the Americas, Pacific Islands, and elsewhere (Vestal & Schultes 1939; Carlson & Jones 1940; Whitehead & Flynn 2017; BRIT 2020; GBIF 2020). The widespread use and cultural importance of the genus *Sapindus* may be reflected in the variety of names applied to it, including but not limited to abolillo, amole, amolillo, att-dtok-ko-ai-od-la, boliche, cherioni, chirrión, guayul, jaboncillo, mata muchacho, palo blanco, soapnut, and wingleaf soapberry (SEINet 2020; BRIT 2020; GBIF 2020). The smooth black seeds of soapberry (Fig. 3) can be polished and used to make beads. The seeds also contain high concentrations of saponins, detergent-like chemicals used to make soap. Medical applications of the chemicals found in soapberry for a range of skin and other conditions have been the subject of several recent studies (Albiero et al 2002; Tsuzuki et al. 2007; García et al. 2012; Rodríguez-Hernandez et al 2016). In southeastern Arizona, the use of soapberry wood by native Americans for crafting arrows was described by European observers in the early twentieth century (Castetter & Underhill 1935). Soapberry has been utilized as a landscaping plant with notably few problems (Hodel 2012; Silva et al. 2018), though some issues with an introduced species of soapberry borer (*Agrilus prionurus*) have been reported in Texas (Billings et al. 2014).

Only *Sapindus saponaria* var. *drummondii* is known to occur Arizona, the northwest extent of the native range of *Sapindus* in the Americas (Figs. 1–2). The closely related and possibly intergrading taxon, *S. saponaria* var. *saponaria* reaches its northernmost extent in Sonora (Fig. 1). However, there are different taxonomic interpretations of the variation within the American Southwest (Kearney & Peebles 1960; Shreve & Wiggins 1964; Felger et al. 2001; Felger & Rutman 2016).

Leaves of soapberry (Figs. 3–4) might be confused with other native and naturalized trees and shrubs with compound leaves, including chinaberry (*Melia azedarach*), smooth sumac (*Rhus glabra*), tree-of-heaven (*Ailanthus altissima*), walnut (*Juglans major*), and ash (*Fraxinus* spp.). The fruits of soapberry are particularly similar in size and color to the fruits of chinaberry, a fairly widespread, non-native tree in Arizona that is both naturalized and widely cultivated. Both *Melia* (Meliaceae) and *Sapindus* (Sapindaceae) belong to the order Sapindales and have compound leaves and panicled

inflorescences. Confusingly, both *Melia* and *Sapindus* have been called by the common name "chinaberry." A helpful point of distinction between the two species is that the tissue of soapberry fruits becomes translucent with age (Fig. 3), while the mature fruits of chinaberry remain opaque.

Soapberry thickets are ecologically important in Arizona, as they provide habitat for a variety of plants and animals. In particular, *Sapindus saponaria* var. *drummondii* is the only known host species for the soapberry hairstreak butterfly, *Phaeostrymon alcestis*. This butterfly is the only member of its genus and is endemic to northern Mexico, Arizona, New Mexico, Texas, and Oklahoma, with a distribution closely overlapping that of its host plant (Fig. 5). The miniscule green caterpillars of the soapberry hairstreak and similar species are well camouflaged against the leaves of their host plant, with nearly identical bright green coloration and hair textures (Warren et al. 2012). Other members of the hairstreak subfamily (Theclinae) such as the commonly observed grey hairstreak, *Strymon melinus*, also utilize soapberry (Fig. 6).

METHODS

For this study, we relied heavily on data hosted by the Southwest Environmental Information Network (SEINet 2020) and the Global Biodiversity Information Facility (GBIF 2020). We referred to aerial imagery associated with known localities to try to identify larger soapberry thickets, especially from the National Agriculture Imagery Program (USDA 2020). We visited approximately 20 different soapberry populations across Arizona in Gila, Mohave, Pima, Pinal, Maricopa, Santa Cruz, and Yavapai counties (Fig. 2) from 2018 to 2020 to take photographs and make general observations. Photographs were taken with a variety of sensors and lenses (including iPhone, Nikon DSLR, and DJI Mavic). Photos were processed in Adobe Lightroom and Photoshop. Cartography layouts were created in QGIS. Drone flights were performed at study sites 1–3. Drone flights within Buenos Aires National Wildlife Refuge (study site 2) were performed under federal permit #2019-013.

We follow Shreve and Wiggins (1964) in recognizing two varieties of soapberry, *Sapindus saponaria* var. *saponaria* and *S. saponaria* var. *drummondii*, with the caveat that the latter "narrow-leafed form grades into the blunter larger leaflet of the typical plants" (Shreve & Wiggins 1964). Because of this apparent gradation and poorly understood taxonomic boundary, Salywon (1999) proposed discarding the varieties and recognizing one morphologically variable species, *Sapindus saponaria*, with a distribution stretching from Argentina to Kansas. In contrast, Felger et al. (2001) recognized both *S. saponaria* and *S. drummondii* at the rank of species, with distinctions noted in leaf morphology, habit, and cold tolerance, stating that "*S. saponaria* differs from *S. drummondii* in nearly always having a much larger well-developed trunk, having much larger and drought deciduous (rather than winter-deciduous) leaves with conspicuously winged leafstalks, slightly larger fruits, and being frost sensitive" (Felger et al. 2001). Felger et al. noted that the "northern range of *S. saponaria* is undoubtedly limited by winter cold; [since] in cultivation it perishes with moderate freezing."

STUDY SITES AND ILLUSTRATIONS

Soapberry has been found between approximately 520 to 2400 meters elevation in Arizona, though the majority of known populations occur between 700 to 1800 meters (SEINet 2020; GBIF 2020). Soapberry habitat varies greatly but generally includes washes and rocky places. In some situations, soapberry thickets may indicate the presence of persistent groundwater (Whitehead & Flynn 2017).

Soapberry tends to occur in clusters spreading outward by rhizomes, evidenced by the commonly observed phenomenon of younger stems arising along the edges of these thickets.

Soapberry thickets that contain several thousand stems and form canopies that tend to be associated with mesquite bosques dominated by velvet mesquite (*Prosopis velutina*) and occasional netleaf hackberry (*Celtis reticulata*). Within these mesquite bosques, soapberry canopy is visually distinct with lighter green foliage.

Flowering in soapberry thickets typically occurs June through August. Fruits form in the fall and often persist through the winter. Older soapberry stems within a clonal thicket seem to produce the most flowers and fruits, while younger individuals often produce no flowers. This phenomenon is evident in Figures 17 and 18.

Western Yellow-billed Cuckoo, a U.S. federally protected species that is listed as threatened, has been observed utilizing habitats within and adjacent to study sites 1 and 2.

Study site 1

The 7B Ranch soapberry thicket study site (Figs. 2, 7–10) is situated along the floodplains of the Lower San Pedro River basin, near Mammoth, Arizona, at approximately 725 m elevation with a center point estimated at 32.70897° N, 110.62100° W. The 7B soapberry thicket itself occupies an area of approximately 1,000 m^2 and contains an estimated 5,200 live soapberry stems. The thicket occurs within an old-growth mesquite bosque. The oldest soapberry tree here is taller than other canopy dominant species (*Prosopis velutina* and *Celtis reticulata*) with an approximate height of 20 m and a DBH (diameter at breast height) of 47 cm. Figure 10 shows the trunk of this individual. Study site 1 may represent the largest soapberry thicket currently known to occur in Arizona, based on what has been recorded in herbarium records and other published records examined.

The understory and adjacent mesquite bosque at study site 1 support a relatively large population of Mexican passionflower (*Passiflora mexicana* Juss.), a species with a fairly limited range and number of known occurrences in the USA (southern Arizona only) and Mexico (SEINet 2020; GBIF 2020).

Study site 2

The Las Guijas soapberry thicket (Figs. 2, 11–14) is situated along Las Guijas Wash in the Beunos Aires National Wildlife Refuge near the USA–Mexico border at approximately 1,020 m elevation with a center point estimated at 31.68459° N, 111.40765° W. The Las Guijas thicket occupies an area of approximately 1,500 m^2 and contains an estimated 3,000 live soapberry stems. The Las Guijas thicket has an approximate maximum canopy height of 6 m, with larger individual trunks up to 20 cm DBH. The soapberry canopy appears slightly shorter than surrounding mesquite and netleaf hackberry canopies. Study site 2 may represent the second largest soapberry population cluster currently known to occur in Arizona, based on what has been recorded in available sources.

Study site 3

The Gardner Canyon soapberry thickets (Figs. 2, 4–5, 15–18) are dispersed in lower Gardner Canyon in the Coronado National Forest at approximately 1,400 m (4,870 ft) elevation with a center point estimated at 31.72697° N, 110.70113° W. This site was not fully surveyed but contains an estimated 2,000 live soapberry stems. Maximum canopy height is approximately 6 m. Common trees in the immediate vicinity include velvet mesquite (*Prosopis velutina*), desert willow (*Chilopsis linearis*), Arizona walnut (*Juglans major*), and Emory oak (*Quercus emoryi*).

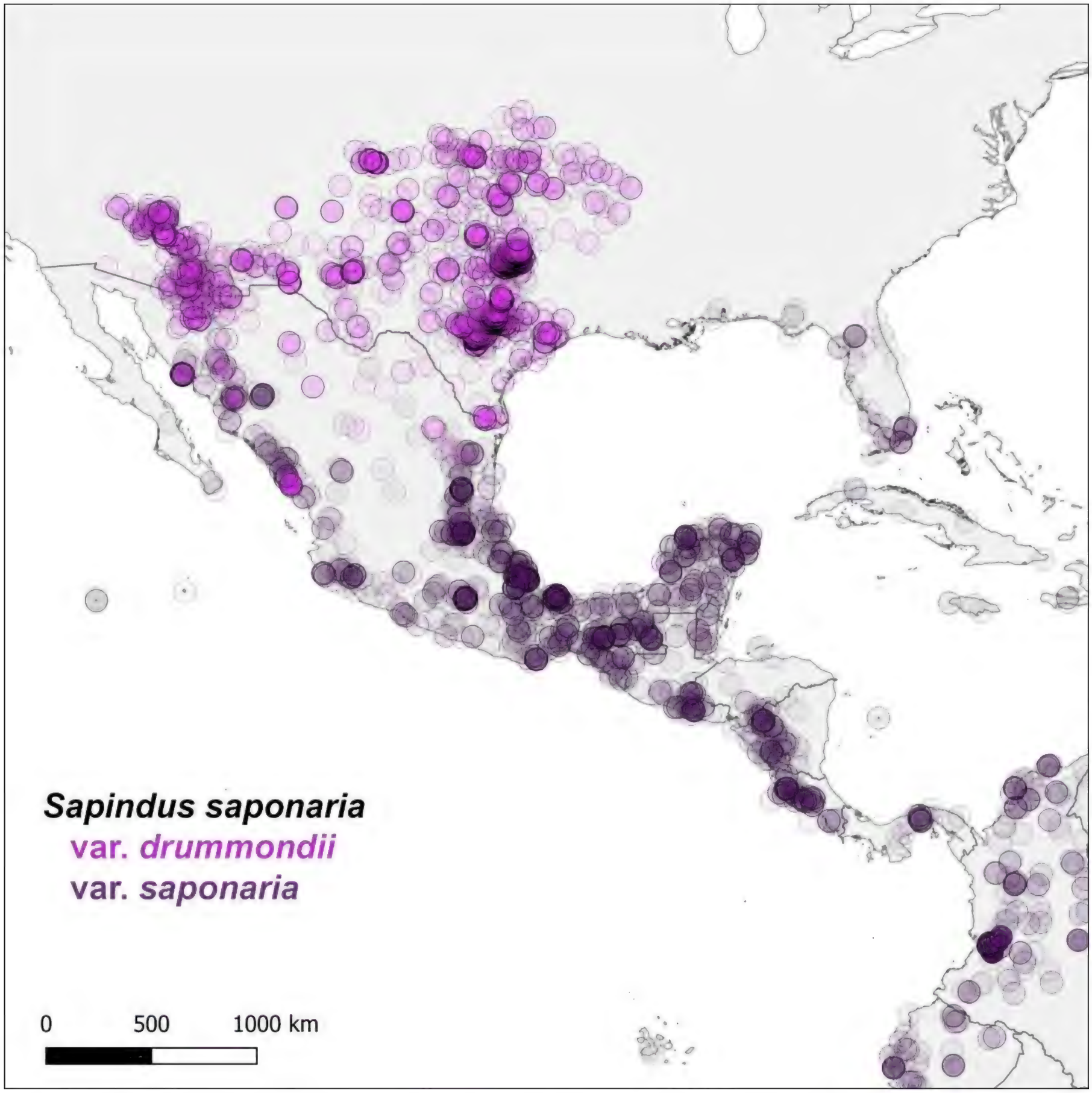

Figure 1. Approximate distribution of the genus *Sapindus* in North America and Central America indicated with semi-transparent circles using data from GBIF (2020) and SEINet (2020). The lighter, violet colored locations represent our interpretation of *Sapindus saponaria* var. *drummondii* distribution, while the darker, purple locations represent our interpretation of *S. saponaria* var. *saponaria* distribution. *Sapindus marginatus* (primarily of Florida) is mapped along with *S. saponaria* var. *saponaria* for the purpose of this visualization.

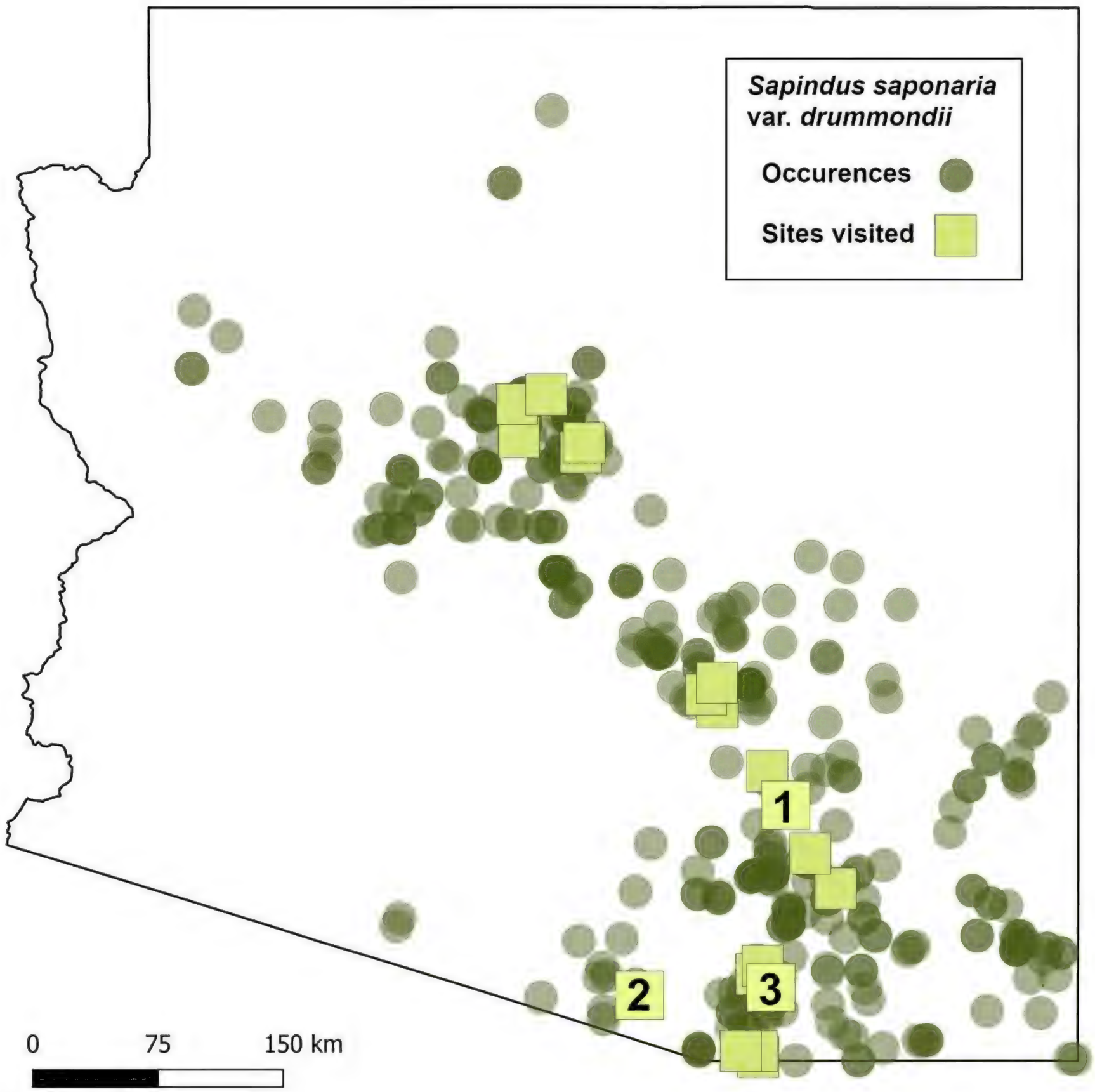

Figure 2. *Sapindus saponaria* var. *drummondii* occurrences in Arizona from the Southwest Environmental Information Network (SEINet 2020), indicated with green semi-transparent circles. All sites visited for this study are indicated with yellow-green squares. Primary study sites 1–3 are indicated.

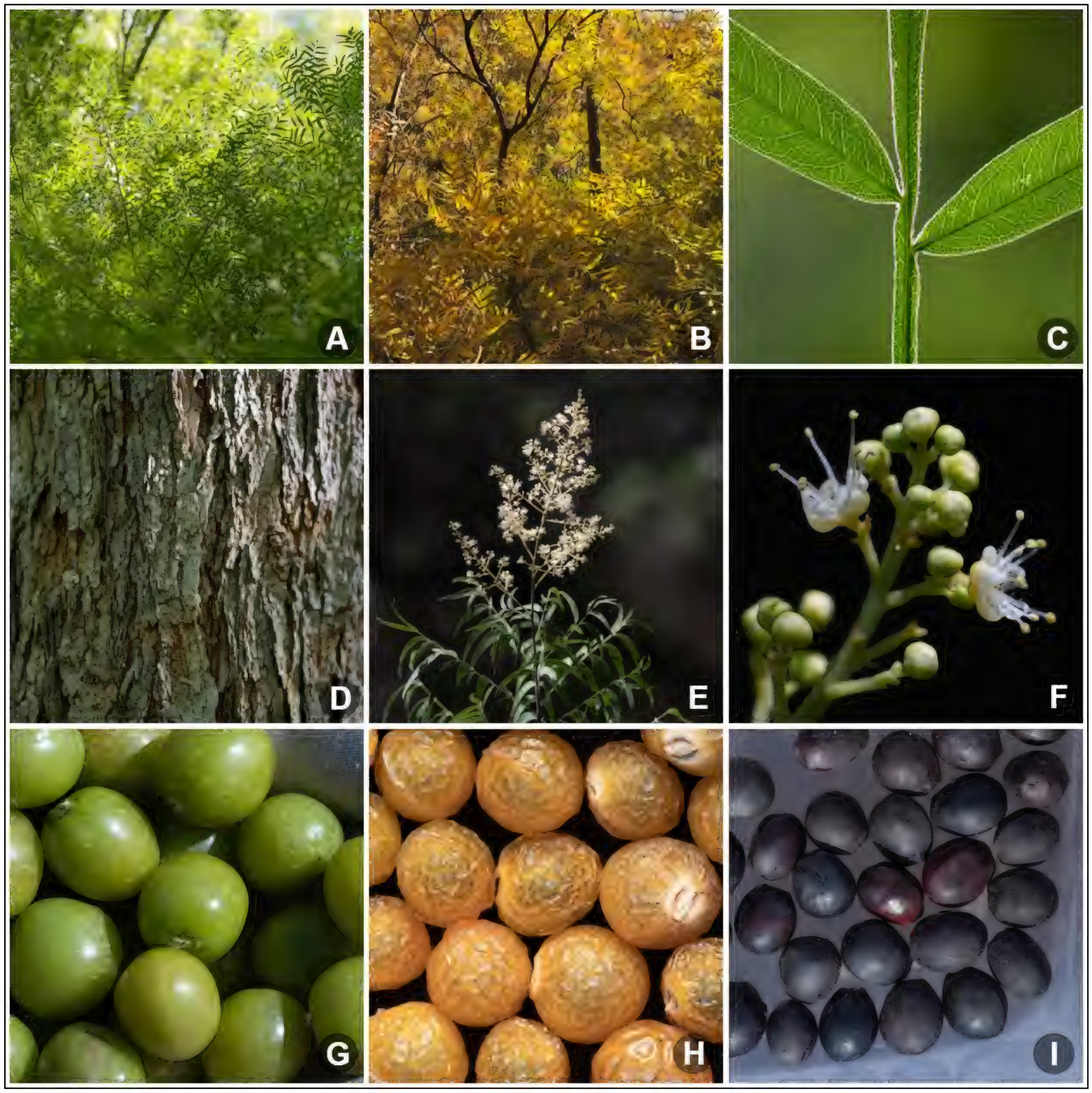

Figure 3. *Sapindus saponaria* var. *drummondii* in Arizona. **A.** Summer leaf colors, looking up into a thicket canopy. **B.** Typical fall leaf colors. **C.** Close-up of winged leaf rachis, present but not as pronounced as others in the genus (note: some leaves lack a winged rachis). **D.** Typical bark of older trees. **E.** Flowers and leaves. **F.** Close-up of flowers with petals measuring approximately 2 mm long. **G.** Opaque (immature) green fruits approximately 1–1.5 cm long. **H.** Translucent (mature) amber-colored fruits approximately 1 cm long. **I.** Reddish-black seeds approximately 0.75 cm long.

Figure 4. *Sapindus saponaria* var. *drummondii* in bloom, 25 June 2020, at study site 3, Coronado National Forest, Arizona.

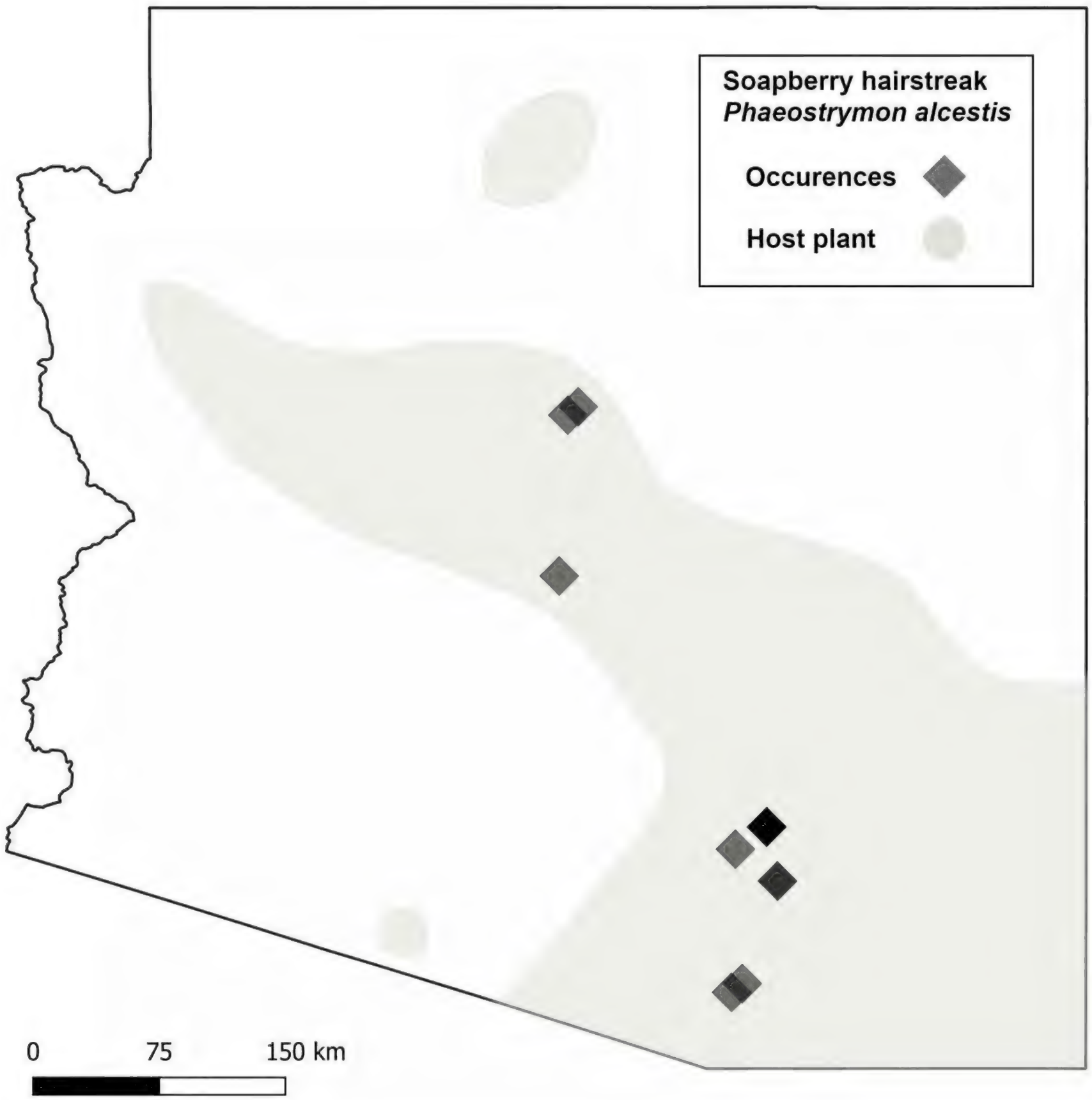

Figure 5. Occurrences of the soapberry hairstreak butterfly (*Phaeostrymon alcestis*) in Arizona (GBIF 2020) with approximate range of its obligate host plant, *Sapindus saponaria* var. *drummondii*.

Figure 6. Floral visitors on *Sapindus saponaria* var. *drummondii* in Arizona, 25 June 2020, at study site 3, Coronado National Forest, Arizona. Floral visitors visible in this photograph include several grey hairstreak butterflies (*Strymon melinus*) and a number of different beetle, bee, and wasp species.

Figure 7. *Sapindus saponaria* var. *drummondii* at study site 1, the 7B Ranch soapberry thicket in Arizona, with an arrow indicating the lighter green signature of the soapberry canopy, at approximately 32.70897° N, 110.62100° W. Imagery is from National Agriculture Imagery Program (NAIP), acquired 19 October 2019 (USDA 2020), displayed in natural color.

Figure 8. *Sapindus saponaria* var. *drummondii* at study site 1, the 7B Ranch Soapberry thicket in Arizona, 12 July 2019, from a drone. Arrows indicate the relatively lighter, yellow-green soapberry canopy appearance during summer months compared with the surrounding bluer mesquite canopy.

Figure 9. *Sapindus saponaria* var. *drummondii* at study site 1, the 7B Ranch soapberry thicket in Arizona, using a telephoto lens from the cliffs along South River Road, 10 May 2019. An arrow indicates the soapberry canopy, which is concentrated in the center of this image and rises above the surrounding canopy to a height of approximately 20 m. The surrounding canopy is composed primarily of velvet mesquite (*Prosopis veluntina*), which dominates the foreground of the image.

Figure 10. *Sapindus saponaria* var. *drummondii* at study site 1, the 7B Ranch soapberry thicket in Arizona, 21 February 2019, illustrating the winter deciduous habit of soapberry thickets. All leaves and stems visible in this photograph are soapberry.

Figure 11. *Sapindus saponaria* var. *drummondii* at study site 2, the Las Guijas Wash Soapberry thicket in Buenos Aires National Wildlife Refuge, Arizona, at approximately 31.68459° N, 111.40765° W. Imagery is from National Agriculture Imagery Program (NAIP), acquired 19 October 2019 (USDA 2020), displayed in natural color. An arrow indicates the soapberry canopy, which is difficult to distinguish from the surrounding mesquite canopy when viewed at this scale.

Figure 12. *Sapindus saponaria* var. *drummondii* at study site 2, the Las Guijas Wash Soapberry thicket in Arizona, 13 July 2019, from a drone. Arrows indicate the yellow-green soapberry canopy signature in contrast with the surrounding blue-green mesquite canopy.

Figure 13. *Sapindus saponaria* var. *drummondii* at study site 2, the Las Guijas Wash soapberry thicket in Arizona, 13 July 2019, from a drone. Arrows indicate the soapberry thicket, which is a lighter, yellower green compared to the surrounding canopy and is concentrated in the foreground, rising to a canopy height of approximately 6 m.

Figure 14. *Sapindus saponaria* var. *drummondii* at study site 2, the Las Guijas Wash soapberry thicket in Arizona, 31 January 2019. The image illustrates the winter deciduous habit of soapberry thickets. All stems and leaves visible in this photograph are soapberry.

Figure 15. *Sapindus saponaria* var. *drummondii* at study site 3, the Gardner Canyon soapberry thicket within the Coronado National Forest, Arizona, at approximately 31.72697° N, 110.70113° W. Imagery is from National Agriculture Imagery Program (NAIP), acquired 19 October 2019 (USDA 2020), displayed in natural color. Arrows indicate the soapberry canopy.

Figure 16. *Sapindus saponaria* var. *drummondii* at study site 3, the Gardner Canyon soapberry thicket in Arizona, from a drone, 25 June 2020. Arrows indicate the soapberry canopy.

Figure 17. *Sapindus saponaria* var. *drummondii* at study site 3, the Gardner Canyon soapberry thicket in Arizona, from a drone, 25 June 2020. Arrows indicate the soapberry canopy. Flowering is mostly restricted to older individuals within the thickets.

Figure 18. *Sapindus saponaria* var. *drummondii* at study site 3, the Gardner Canyon soapberry thicket, 25 June 2020.

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Funding for this research was provided by Resolution Copper. The 7B Ranch (study site 1) is currently owned by Resolution Copper and managed by the Nature Conservancy. Under the terms of federal legislation passed in 2014, the Southeast Arizona Land Exchange and Conservation Act, Resolution intends to transfer ownership of the 7B Ranch to the Bureau of Land Management.

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LOBELIA BATSONII (CAMPANULACEAE), A NEW SPECIES FROM THE SANDHILLS OF THE CAROLINAS

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ABSTRACT

Lobelia batsonii A.B. Pittman & Sorrie, **sp. nov.**, is described from the Sandhills Region of the Carolinas. It previously has been identified as *L. glandulosa* Walt. but differs in a number of features, notably the glabrous interior of corolla tube and throat and the suberose outer seed coat. Supporting data are provided, along with cited specimens and a distribution map.

In recent years references have been made to an undescribed *Lobelia* in the Sandhills Region of North and South Carolina (Amoroso & Finnegan 2002; Sorrie et al. 2006; Sorrie 2011; Spaulding et al. 2016; Weakley 2018). In this paper we provide a name for this new species — *Lobelia batsonii* A.B. Pittman & Sorrie — and describe its morphological and ecological characteristics.

Pittman first recognized this entity as similar to *Lobelia glandulosa* Walt. but as differing in several points. In a letter to Sorrie (undated, mid 1990s), he stated that "the new lobelia is close to *L. glandulosa* which is distinctly hirsute in the throat of the corolla. Fernald (1947) described variety *laevicalyx,* but throat is still hirsute inside." Here Pittman was alluding to the primary distinguishing character of *L. batsonii*: the glabrous interior of corolla tube and throat. Subsequent research revealed the presence of a soft corky seed coat in late season plants unlike any other *Lobelia* in the Carolina flora.

A search by the authors through various herbaria has uncovered specimens of *Lobelia batsonii* dating back to the mid-1800s, e.g., South Carolina, undated, *M.A. Curtis s.n.* (GH, annotated by Pittman). Once botanists were alerted by Pittman in the 1990s to the new species' habitat and morphology, many populations were found throughout the Sandhills Region (Map 1).

LOBELIA BATSONII A.B. Pittman & Sorrie, **sp. nov. TYPE**: **South Carolina**. Lexington Co.: Shealy's Pond Heritage Preserve, 1.5 mi W of community of Edmund on SC Secondary Rd 279, mature white cedar swamp along Scouter Creek, forming clones in seepages and springheads lined with peatmoss hummocks, also in mucky soils along pond margins, 19 Oct 1991, *A.B. Pittman 10199101* (holotype USCH, Fig. 1; isotypes CU!, DUKE!, GH!, MO!, NCU!, NY!).

Most similar to *Lobelia glandulosa* but differing notably in the glabrous calyx, glabrous corolla tube interior and throat (vs. densely pubescent), and in generally smaller dimensions.

Perennial herb, usually(?) producing early season basal offsets and stolons. Stems and leaves glabrous, unbranched or few-branched. Offsets and basal leaves short to long-petioled, lanceolate to elliptical or orbicular, usually absent at anthesis. Cauline leaves 3–15, well-spaced, sessile, blades linear to lanceolate, 20–100 x 2–10 mm, margins denticulate to subentire. Inflorescences 3–15 flowered, unbranched, secund. Pedicels 3–10 mm, 2-bracteolate basally. Sepals glabrous, lobes linear to very narrowly triangular, 5–10 mm, entire. Corolla pinkish blue to lavender blue, with white eye and 2 white guidelines, 17–22 mm including lobes, corolla tube 9–10 mm, fenestrate, base of lower lip and interior of tube glabrous. Filament tube 7.0–8.5 mm, anther tube 3.5–4.0 mm, apically tufted with white hairs. Capsules ascending, 6–7 mm. Seeds 0.9–1.0 mm, outer seed coat suberose.

We are pleased to name this plant after Wade T. Batson (1913-2015), for 30 years Professor of Botany at the University of South Carolina in Columbia, mentor to many undergraduate and graduate students and a lifelong student of the flora of the Carolinas.

Additional specimens examined (due to Covid-19 restrictions, not all specimens assigned a repository have yet been distributed). **North Carolina.** Cumberland Co.: Fayetteville city watershed land, NW end of Bonnie Doone Lake, saturated floor of narrow swamp forest, 27 May 1998, *Sorrie 9745* (NCU, AMAL). Harnett Co.: margin of artificial pond, 10.6 miles E of Lee County line on U.S. 421, 18 Oct 1956, *Laing 628* (NCU). Hoke Co.: Fort Bragg, wet streamhead, NW branch of Mott Lake at firebreak 14, 8 Sept 1992, *Sorrie 6925* (NCSC); Fort Bragg, seepy mucky edge of shrubby streamhead, S of firebreak 29, 11 Sept 1993, *Sorrie 7659* (AMAL); Fort Bragg, outlet at S end of Mott Lake, *Taxodium ascendens-Nyssa biflora* swamp, 30 Sept 1993, *Sorrie 7727* (NCU, GH); Fort Bragg, Deep Creek swamp S of firebreak 18, in pools and rivulets, 2 Aug 2000, *Sorrie 10581* (US); Fort Bragg, former borrow pit, now a wet gladey swamp with *Decodon*, 150 plants all basal leaves, 9 Aug 2000, *Sorrie, Hall, & Hoffman* (sight record); Fort Bragg, boggy glade just below beaver dam at western third of Green Spring Pond, 10 Aug 2000, *Sorrie & Hall 10595* (US); Fort Bragg, East Fork Deep Creek at firebreak 22, 27 Sept 2000, *Sorrie & Hall 10632* (GA, NCU, USCH); Quewhiffle Preserve, 29 Sept 2002, *Sorrie 11021* (BRIT); Calloway Preserve, unnamed tributary of Mill Creek, with *Coreopsis gladiata* s. str., *Lycopus cokeri*, 9 Sept 2019, *Sorrie et al. 13770* (NCU). Moore Co.: Pinehurst, 1897, *Katzenstein s.n.* (GH); Niagara, common in wet sphagnum of ditch at base of seepage slope, Niagara-Carthage Road near McDeed's Creek, 29 Sept 2002, *Sorrie 11023* (NCU); in powerline, boggy margin of beaver pond in Nick's Creek, 22 Oct 2019, *Sorrie et al. 13795* (MO, NCU). Richmond Co.: Sandhills Game Land, NW of Six Corners, 7 Oct 1997, *Sorrie 9595* (NCU); Sandhills Game Land, just E of Deatons Lane and S of Naked Creek Lane, wet sphagnous streamhead, 26 Aug 1998, *Sorrie 9919* (NCU, USCH); Sandhills Game Land, N side of Nursery Lane, headwaters of Bones Fork, 14 Oct 1998, *Sorrie 10021* (GH, NCU); Sandhills Game Land, shortly S of Nursery Lane, headwaters of Bones Fork, 14 Oct 1998, *Sorrie 10022* (US, USCH). Scotland Co.: Sandhills Wildlife Management Area, 4.7 miles SSE of Hoffman on Broadacres Lake Road, 21 Sept 1958, *Gupton 971* (NCU). **South Carolina.** Chesterfield Co.: Cheraw State Park, peat-sedge bog, 29 Sep 1956, *Radford 18639* (NCU). Darlington Co.: Segars Mill Pond, 5 Oct 1940, *Smith 1398* (NCU); same place, 20 Sep 1940, *Smith 1400* (NCU); Society Hill, 1 Oct 1940, *Smith 1399* (NCU); Hartsville, 28 Sept 1909, *Coker s.n.* (NCU); same place, 9 Oct 1909, *Coker s.n.* (NCU); Hartsville, Prestwood Lake, 10 Nov 1921, *Norton s.n.* (NCU); Hartsville, along shores of Black Creek pond, 20 Nov 1921, *Norton s.n.* (US); Hartsville, 5 Oct 1940, *B.E. Smith 1397* (NCU). Lexington Co.: Bog near Scouter Creek, 2 miles W of Edmund, 5 Oct 1957, *Radford 29844* (NCU); W of Pelion, downstream from US 178, on log in impoundment in drainage of Black Creek, 24 Sept 2011, *Nelson 30087* (USCH). Richland Co.: Wet bog near Columbia, 26 Sep 1883, *Donnell Smith s.n.* (GH, MO). **No county** named, no date, *M.A. Curtis s.n.* (GH).

Lobelia batsonii is restricted to the Sandhills Physiographic Region of North and South Carolina (Fenneman 1938). It is not known to occur on the younger sediments of the flatter portions of the Coastal Plain (to the east of the Sandhills) nor is it known to be syntopic with *L. glandulosa*. Botanists should also search adjacent Georgia for *L. batsonii*. Flowering late August to mid October, occasionally until frost.

Map 1. Distribution of *Lobelia batsonii*.

Lobelia batsonii is found in a narrow suite of habitats. Primarily, it occupies perennially saturated, sphagnous, blackwater streamheads under open to closed canopy of *Acer rubrum*, *Nyssa biflora*, *Liriodendron tulipifera*, and *Chamaecyparis thyoides*. Associates include *Asclepias rubra*, *Cyrilla racemiflora*, *Doellingeria sericocarpoides*, *Eupatorium resinosum*, *Gentiana catesbaei*, *Juncus trigonocarpus*, *Lindera subcoriacea*, *Lycopus cokeri*, *Lyonia lucida*, *Solidago salicina*, *Zenobia pulverulenta*, and the recently described *Carex austrodeflexa*. Plants occupy the wettest zones with sphagnum moss and also laterally into the shrub-graminoid ecotone of the longleaf pine-wiregrass community, especially where disturbance such as a road or a trail has opened the canopy. Beavers often create ponds in the same streams, sometimes with *L. batsonii* in the upslope margins. Plants also occur in more or less isolated areas of seepage, including pitcher plant seepage slopes. Elevations range from 50-200 meters.

Figure 1. *Lobelia batsonii*. Holotype, *Pittman 10199101* (USCH).

Figure 2. *Lobelia batsonii*, leaves and lower stem. Moore Co., North Carolina, September 2020. Photo by B.A. Sorrie

Figure 3. *Lobelia batsonii* inflorescence, Moore Co., North Carolina, September 2020. Photo by Sorrie.

Figure 4. Top (left) *Lobelia batsonii* — short corolla tube, photo by Sorrie; (right) *Lobelia glandulosa* — long corolla tube, photo by J. Pippen. Bottom (left) *Lobelia batsonii* — lack of pubescence at corolla mouth, photo by Sorrie; (right) *Lobelia glandulosa* — pubescence extending out from corolla mouth, photo by J. Pippen.

Table 1 compares a number of characters that separate *Lobelia batsonii* from *L. glandulosa*. Fernald (1947), and others have confused *L. elongata* Small with *L. glandulosa* and the new species, but *L. elongata* is highly distinct in its broadly lanceolate to elliptical leaves, longer and denser inflorescence, glabrous exterior of calyx tube, and pubescent interior of corolla tube. In the field, one would never confuse *L. elongata* with either *L. glandulosa* or *L. batsonii* (see images of *L. elongata* and *L. glandulosa* in Spaulding and Barger 2016). McVaugh (1936) mentioned seeing some specimens of *L. glandulosa* "... with nearly or wholly entire leaves and lobes of the calyx" [i.e. without glandular teeth]. Fernald (1947) named such plants *L. glandulosa* var. *laevicalyx* Fern.; as Table 1 indicates, they are clearly aligned with species *L. glandulosa* and not with *L. batsonii*.

Table 1. Primary morphological and habitat characters of *Lobelia batsonii* and *L. glandulosa*. For measurements, n = 25.

Character	***L. batsonii***	***L. glandulosa*** var. ***glandulosa***	***L. glandulosa*** var. ***laevicalyx***
Cauline leaves	linear, occasionally lanceolate	linear, occasionally lanceolate	linear, occasionally lanceolate
Inflorescence	sparsely flowered to moderate	sparsely flowered	sparsely flowered
Calyx tube pubescent externally	no	yes	no or glabrate
Calyx lobes glandular-toothed	no	long to short, occasionally no	long to short, occasionally no
Corolla length (mm)	17–22	19–27	19–27
Corolla tube pubescent within, and proximal to orifice	no	yes, usually densely hirsute	yes, usually densely hirsute
Seed coat	tuberculate-alveolate, suberose, soft	tuberculate-alveolate, cartilaginous	tuberculate-alveolate, cartilaginous
Habitat	wet mossy streamheads, ecotones, seepage slopes along streams, black-water impoundments	wet flatwoods, savannas, seepages	wet flatwoods, savannas, seepages

In addition to the contrasts in Table 1, plants of *Lobelia batsonii* tend to be shorter (maximum 80 cm vs. 140 cm in *L. glandulosa*), have shorter and narrower cauline leaves (maximum 100 mm vs. 150 mm long; maximum 10 mm vs. 14 mm wide), shorter sepals (maximum 10 mm vs. 15 mm), shorter corolla tubes (maximum 10 mm vs. 12 mm), and shorter filament tubes (maximum 8.5 mm vs. 12 mm). Data are from the FNA draft treatment of *Lobelia glandulosa* (Lammers 2020) and from specimens of *L. batsonii* examined by the authors.

Finally, we call attention to the presence of basal leaves, seen in the holotype (Fig. 1) and a few other specimens, a character not mentioned in the literature for *Lobelia glandulosa* sensu lato. They are present early in the growing season (March-May), occurring as well-spaced, elliptical blades with well-developed petioles, but sometimes clustered together as "rosettes" with orbicular leaves and short petioles. Whitish stolons suggest a perennating habit reminiscent of *Eryngium prostratum* Nutt. ex DC. We have seen only a handful of specimens with such basal leaves and stolons. A search of online specimens at several herbaria confirms that early season basal leaves also occur in *L.*

glandulosa. However, the tiny percentage recorded (1.6%) renders any statements about significance moot, and we recommend that additional studies be conducted.

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MECARDONIA PROCUMBENS (PLANTAGINACEAE) NEW TO THE FLORA OF MISSISSIPPI

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ABSTRACT

The first known occurrence in Mississippi of *Mecardonia procumbens* is reported here. The plants were in a disturbed area on the United States Army Corps of Engineers Engineer Research and Development Center campus in Warren County. A photograph of a specimen in situ is provided.

Two plants of *Mecardonia procumbens* (Miller) Small (baby jump-up, yellow water-hyssop) (Fig. 1) were discovered in 2020 in Warren Co., Mississippi. They were mature individuals established in a previously disturbed area. No additional specimens were observed during a search of the general vicinity around roads, sidewalks, and parking areas. Based on the overall distribution of the species in the USA (Fig. 2), however, it probably already occurs elsewhere in Mississippi.

Figure 1. *Mecardonia procumbens* growing near the edge of a road and parking area interface, Warren Co., Mississippi.

Voucher specimen. Mississippi. Warren Co.: Vicksburg, United States Army Corps of Engineers Engineer Research and Development Center campus, N side of Chesapeake Road, S of intersection with Tennessee Road, 32.29701° N, 90.86993° W, two plants near the edge of the road and parking area interface, with *Eragrostis cilianensis*, *Euphorbia maculata*, *Leucospora multifida*, and *Mollugo verticillata*, 19 Aug 2020, *Philley 2205* (ERDC).

Mecardonia procumbens is considered native to tropical and subtropical portions of the Americas but has become established on every continent except Antarctica (Plants of the World Online 2019). Kartesz (2015) and USDA,NRCS (2020) depict its range in the continental USA as occurring from southern Arizona to Florida. Recent collections from Arkansas (in 2013 and 2016) and South Carolina (in 2016) have expanded the known distribution represented in these sources. A search of the SERNEC Data Portal (2020) resulted in additional county records in states where *M. procumbens* had been documented previously. A composite distribution map based on these three sources and the new locality in Warren Co., Mississippi, is shown in Figure 2.

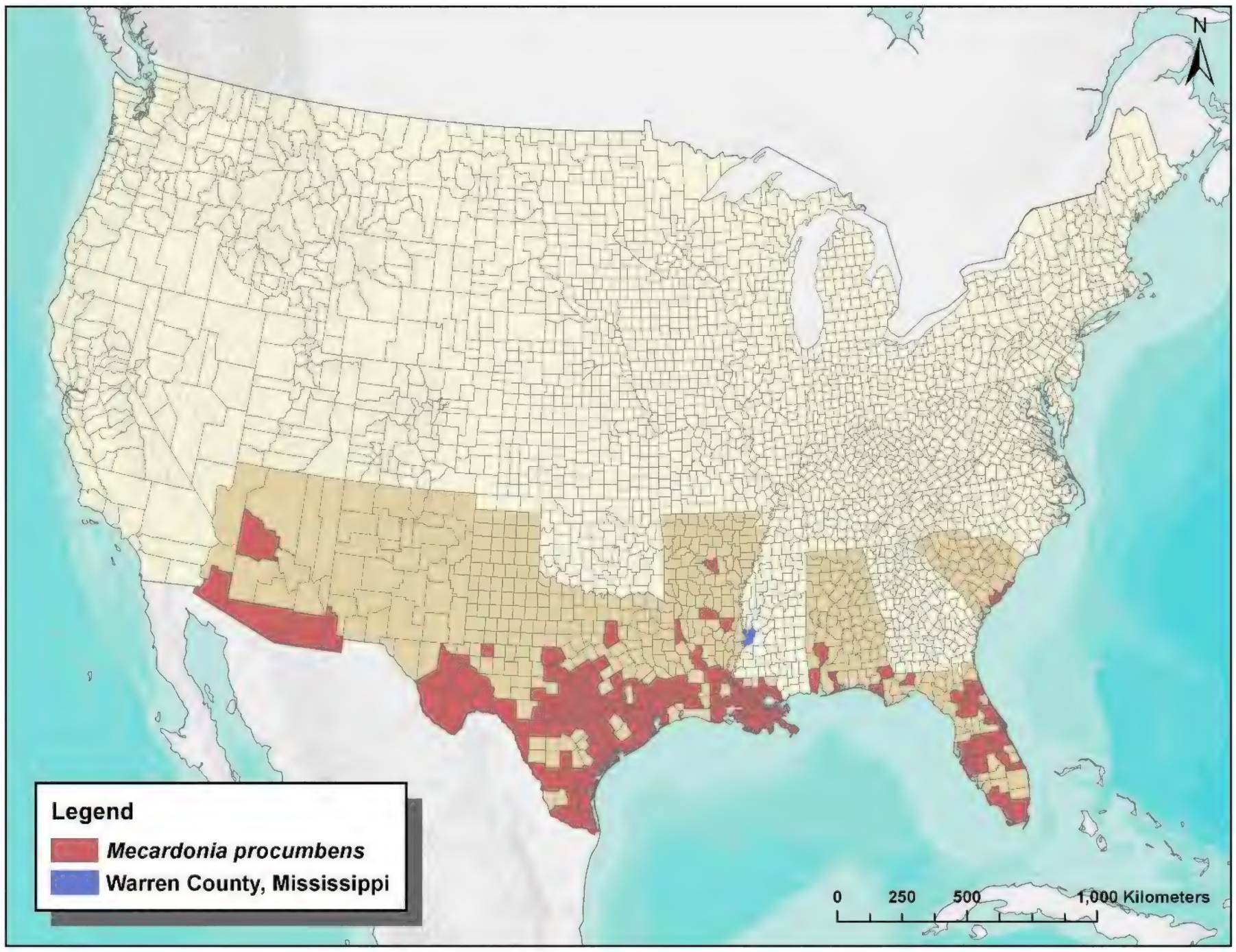

Figure 2. Composite distribution map of *Mecardonia procumbens* in the continental USA based on Kartesz (2015), USDA,NRCS (2020), SERNEC Data Portal (2020), and the new locality in Warren Co., Mississippi.

Mecardonia procumbens is considered a wetland plant wherever it occurs in the USA (Lichvar et al. 2016). It is considered a facultative wetland hydrophyte (usually occur in wetlands, but may occur in non-wetlands) in all regions with the exception of the Atlantic and Gulf Coastal Plains (AGCP), where it is considered an obligate wetland hydrophyte (almost always occur in wetlands). However, many of the records from disturbed localities in the AGCP, including the site in Warren County, may lack wetland hydrology, hydrophytic vegetation, and hydric soils. These descriptions suggest that a review of its wetland indicator status within the AGCP region is needed —*M. procumbens* perhaps should be regarded as a facultative wetland hydrophyte.

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A PHYLOGENY OF THE HUBBARDOCHLOINAE INCLUDING *TETRACHAETE* (CYNODONTEAE: CHLORIDOIDEAE: POACEAE)

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ABSTRACT

The phylogeny of subtribe Hubbardochloinae is revisited, here with the inclusion of the monotypic genus *Tetrachaete*, based on a molecular DNA analysis using *ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS markers. *Tetrachaete elionuroides* is aligned within the Hubbardochloinae and is sister to *Dignathia*. The biogeography of the Hubbardochloinae is discussed, its origin likely in Africa or temperate Asia.

In a previous molecular DNA phylogeny (Peterson et al. 2016), the subtribe Hubbardochloinae Auquier [*Bewsia* Gooss., *Dignathia* Stapf, *Gymnopogon* P. Beauv., *Hubbardochloa* Auquier, *Leptocarydion* Hochst. ex Stapf, *Leptothrium* Kunth, and *Lophacme* Stapf] was found in a clade with moderate support (BS = 75, PP = 1.00) sister to the Farragininae P.M. Peterson et al. In the present study, *Tetrachaete elionuroides* Chiov. is included in a phylogenetic analysis (using *ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS DNA markers) in order to test its relationships within the Cynodonteae with heavy sampling of species in the supersubtribe Gouiniodinae P.M. Peterson & Romasch.

Chiovenda (1903) described *Tetrachaete* Chiov. with a with single species, *T. elionuroides* Chiov. He characterized it as being a dwarf, delicate, xerophilous annual with short leaf blades and greatly amplified (inflated) sheaths partially enclosing short inflorescences, and resembling slender forms of *Elionurus royleanus* Nees ex A. Rich. In addition to the above characters, *Tetrachaete* has narrow, spiciform inflorescences with short racemose branches bearing two sessile, contiguous 1-flowered spikelets, each with two bristle-like glumes, and a coriaceous, gibbous, 3-veined, and short-awned lemma (Clayton et al. 2006). Initially, *Tetrachaete* was placed in the Zoysieae Benth. but was thought not to resemble any current members (Chiovenda 1903).

MATERIALS AND METHODS

Detailed methods for DNA extraction, amplification, and sequencing are given in Romaschenko et al. (2012) and Peterson et al. (2010, 2014a, b, 2015a, b, 2016). We used Geneious Prime 2020 (Kearse et al. 2012) for contig assembly of bidirectional sequences of *ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK*, and ITS regions, and Muscle (Edgar 2004) to align consensus sequences and adjust the final alignment. We identified models of molecular evolution for the cpDNA and nrDNA regions using jModeltest (Posada 2008) and applied maximum-likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined data sets were partitioned in accordance with the number of markers used. Nucleotide substitution models selected by Akaike's Information Criterion, as

implemented in jModelTest v.0.1.1, were specified for each partition. The ML analysis was conducted with GARLI 0.951 (Zwickl 2006). The ML bootstrap analysis used 1000 replicates with 10 random addition sequences per replicate. The tree file from the ML result was read into PAUP where the majority-rule consensus tree was constructed. Bayesian posterior probabilities (PP) were estimated using a parallel version of the MrBayes v3.2.7 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003) where the run of eight Markov chain Monte Carlo iterations was split between an equal number of processors. Bayesian analysis was initiated with random starting trees and was initially run for four million generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences dropped below 0.01 and the potential scale reduction factor was close to or equal to 1.0. The fraction of the sampled values discarded as burn in was set at 0.25.

RESULTS AND DISCUSSION

Three new sequences from two species are reported in GenBank, along with all other species included in this study (Appendix 1). Total aligned characters for individual regions and other parameters are noted in Table 1. The resulting plastid and ITS topologies were inspected for conflicting nodes, and given that none were found, the plastid and ITS sequences were combined.

The ML tree from the combined plastid and ITS regions (Fig. 1) is well resolved (posterior probabilities identified in the Bayesian analysis are included on the ML tree, and most clades include a PP = 1), with strong support (BS = 100) for the following clades: the **Cteniinae** P.M. Peterson, Romasch. & Y. Herrera with a single genus, **Farragininae** P.M. Peterson, Romasch. & Y. Herrera with two genera, **Gouiniinae** P.M. Peterson & Columbus with five genera, **Hubbardochloinae** Auquire with eight genera, **Perotidinae** P.M. Peterson, Romasch. & Y. Herrera with three genera, **Trichoneurinae** P.M. Peterson, Romasch. & Y. Herrera with a single genus, and the **Zaqiqahinae** P.M. Peterson, Romasch. & Y. Herrera with a single genus. These seven subtribes form the Gouiniodinae (PP = 1, BS = 89) previously delimited in Peterson et al. (2014a; 2016).

Tetrachaete elionuroides is clearly aligned within the Hubbardochloinae and is sister to three species of *Dignathia* (PP = 0.96, BS = 73). *Tetrachaete* and *Dignathia* share a cylindrical, spiciform inflorescence with each branch bearing 1 or 2 spikelets, glumes longer than the floret, coriaceous and gibbous 3-veined lemmas that bare an awn or mucro (Clayton & Renvoize 1986; Clayton et al. 2006). *Tetrachaete elionuroides* has recently been classified in the subtribe Unioliinae, tribe Eragrostideae (Soreng et al. 2015, 2017) — the present study is the first to include it within a molecular DNA study. Even though Clayton (1973) previously included *Tetrachaete* within the Zoysieae or Zoysiinae Benth. (Clayton & Renvoize 1986), inclusion within the Unioliinae by Soreng et al. (2015, 2017) probably was a result of confusion with molecular reports for *Tetrachne* Nees, a genus with a strikingly similar orthography. The circumscription of the Zoysieae in the 20th century has changed considerably since Columbus et al. (2007) interpreted it to include the Sporobolinae Benth. and the Zoysiinae sensu stricto with only *Urochondra* C.E. Hubb. and *Zoysia* Willd.

In our new cladogram (Fig. 1) the *Tetrachaete*−*Dignathia* clade is sister to *Leptothrium*, and together they are sister to remaining taxa in the Hubbardochloinae consisting of *Leptocarydion* (basal) sister to the *Bewsia* (*Hubbardochloa*−*Lophacme*) + *Gymnopogon*. This topology is similar to those of earlier studies, and again, *Hubbardochloa* is a weakly supported (PP = 0.95, BS = 69) sister to *Lophacme* (Peterson et al. 2016). This is perhaps a consequence of our data set since we have only ITS sequences for *Hubbardochloa*, but we have additional evidence from At103 sequences (Peterson & Romaschenko, unpublished) that support their union.

Table 1. Characteristics of the five DNA regions, *rps16-trnK, rps16* intron, *rpl32-trnL, ndhA* intron, and ITS, and parameters used in Bayesian analyses indicated by Akaike Information Criterion.

Characteristic	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	Combined plastid data	ITS	Overall
Total aligned characters	954	989	998	1224	4165	822	4987
Number of sequences	77	75	86	63	301	83	386
Likelihood score (-lnL)	4747.48	4160.57	5081.98	5192.84		13353.53	
Number of substitution types	6	6	6	6		6	
Model for among-sites rate variation	gamma	gamma	gamma	gamma		gamma	
Substitution rates	1.08484 2.63283 0.38677 1.69488 2.53685 1.00000	1.05191 1.18636 0.28231 1.35625 1.50278 1.00000	0.95937 1.84326 0.33665 1.64568 1.35965 1.00000	1.41777 2.65062 0.50658 2.00718 2.76826 1.00000		0.93969 2.86085 1.70535 0.65184 4.95421 1.00000	
Character state frequencies	0.31138 0.13354 0.13695 0.39348	0.39017 0.11028 0.16498 0.33271	0.36487 0.13373 0.12286 0.36497	0.36803 0.13454 0.14589 0.35436		0.25255 0.21184 0.24684 0.30716	
Proportion of invariable sites	0.12125	0.28284	0.19469	0.29151		0.26061	
Gamma shape parameter (α)	1.50178	1.12559	1.04856	0.97096		1.02378	

Like *Tetrachaete elionuroides*, the Hubbardochloinae probably originated in Africa, since most species of *Dignathia* and *Leptothrium* (sister to the *Dignathia-Tetrachaete* clade in Fig. 1) are distributed in Africa or temperate Asia (Clayton & Renvoize 1986; Clayton et al. 2006). The Gouiniodinae also probably originated in Africa or Asia, since *Zaqiqah* P.M. Peterson & Romasch. (basal and sister to all other genera in the supersubtribe, see Fig. 1) occurs in Ethiopia, Saudi Arabia, Somalia, Socotra, and Yemen (Peterson et al. 2016). Only *Gymnopogon* with 14 species is composed entirely of western hemisphere species from North and South America, whereas the other seven Hubbardochloinae genera include some species with an African distribution (Peterson et al. 2016; Soreng et al. 2017).

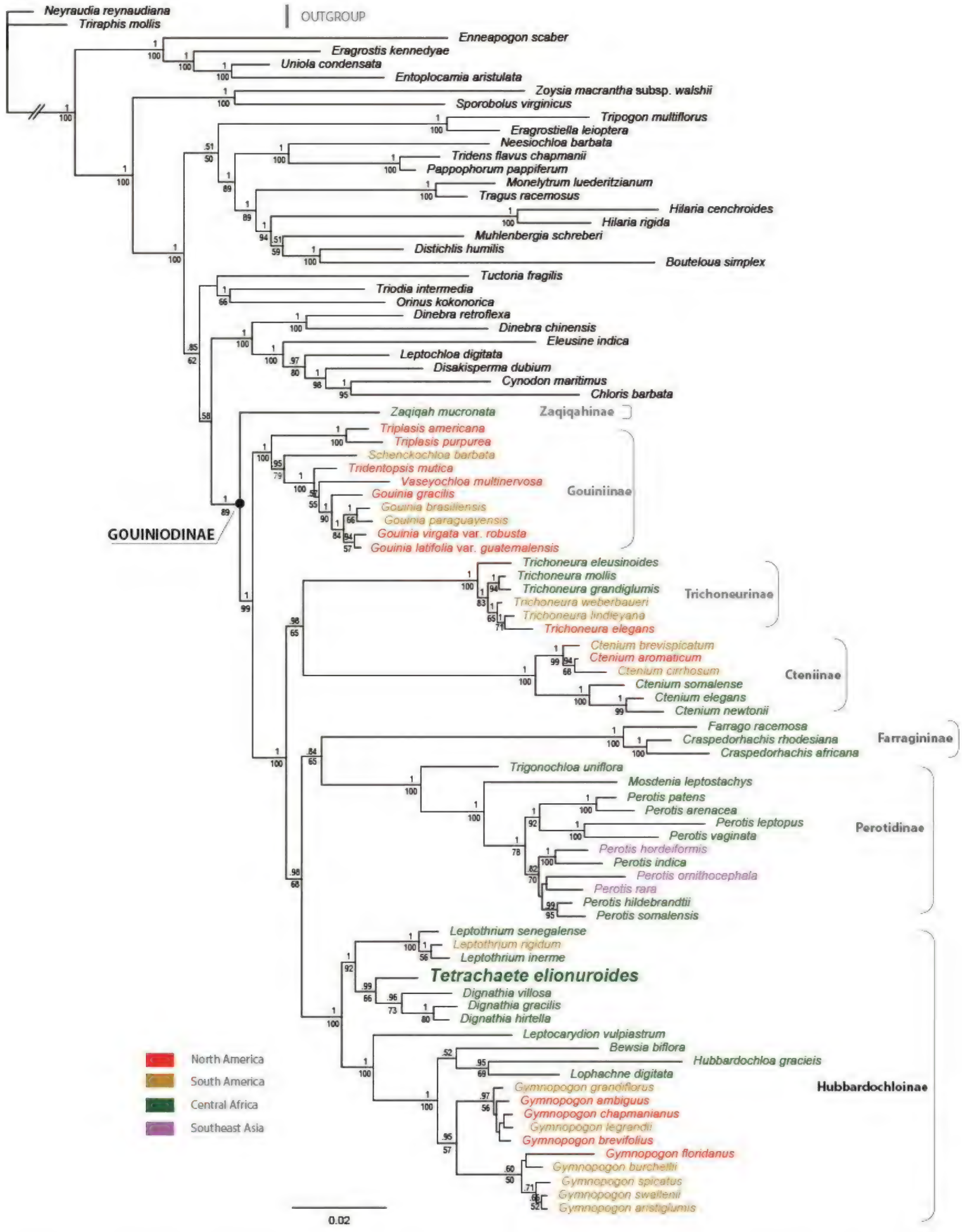

Figure 1. Maximum-likelihood tree inferred from combined plastid (*ndhA* intron, *rpl32-trnL*, *rps16* intron, *rps16-trnK* and ITS sequences. Numbers above branches are posterior probabilities; numbers below branches are bootstrap values; scale bar = 2%.

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Appendix 1. Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of *rps16-trnK, rps16 intron, rpl32-trnL, ndhA intron,* and ITS regions (**bold** indicates new accession); a dash (–) indicates missing data.

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Bewsia biflora (Hack.) Gooss.	Peterson 23905, Soreng, Romaschenko & Abeid (US)	Tanzania, Ruvuma	KF827754	KF827692	KF827617	KF827570	KF827498
Bouteloua simplex Lag.	Peterson 21289, Saarela & Flores Villegas (US)	Mexico, Zacatecas	GU360607	GU360297	GU359834	GU359406	GU359231
Chloris barbata Sw.	Peterson 22255& Saarela (US)	Mexico, Sinaloa	GU360514	GU360435	GU359873	GU359377	GU359320
Craspedorhachis africana Benth.	Laegaard 16192 (US)	Zimbabwe	KF827757	KF827693	KF827620	KF827571	KF827501
Craspedorhachis rhodesiana Rendle	Strohbach 5699 (US)	Namibia	KF827760	KF827696	KF827623	KF827574	KF827504
Ctenium aromaticum (Walter) Alph. Wood	Peterson 14235, Weakley & LeBlond (US)	USA, North Carolina	–	–	GU359839	–	GU359240
Ctenium brevispicatum J.G.Sm.	Filgueiras 3251 & Oliviera (US)	Brazil, Goiás	KF827764	KF827700	KF827627	KF827578	KF827508
Ctenium cirrhosum (Nees) Kunth	Grola 1452 & Filgueiras (US)	Brazil	GU360597	GU360353	GU359838	–	GU359241
Ctenium elegans Kunth	Laegaard 18359, Mipro & Sobere (US)	Burkina Faso	KF827765	KF827701	–	–	KF827509
Ctenium newtonii Hack.	Laegaard 18327, Mipro & Sobere (US)	Burkina Faso, Nazinga Park	KF827767	KF827702	KF827628	KF827579	KF827511
Ctenium somalense (Chiov.) Chiov.	Magogo 279 & Glover (FT)	Kenya, Kwale	KF827769	KF827704	KF827630	KF827580	KF827513
Cynodon maritimus Kunth	Howard 10214 & Howard (US)	Bahamas, Bimini	GU360591	GU360448	GU359889	GU359365	GU359248
Dignathia gracilis Stapf	Greenway 10449 (US)	Kenya	–	–	KF827631	–	–

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Dignathia hirtella Stapf	Barkhadle 353 (FT)	Somalia	KF827770	KF827705	KF827632	KF827581	KF827514
Dignathia villosa C.E. Hubb.	Ellis 204 (US)	Ethiopia	GU360519	GU360480	GU359820	GU359367	–
Dinebra chinensis (L.) P. M. Peterson & N. Snow	Snow 6909 (MO)	Botswana	JQ345240	–	JQ345325	–	JQ345171
Dinebra retroflexa (Vahl) Panz.	Ndegwa 610 (US)	Kenya	GU360503	GU360479	GU359778	GU359355	GU359332
Disakisperma dubium (Kunth) P. M. Peterson & N. Snow	Peterson 22334 & Saarela (US)	Mexico, Oaxaca	GU360695	GU360416	GU359811	GU359442	GU359145
Distichlis humilis Phil.	Peterson 19362, Soreng, Salariato & Panizza (US)	Argentina, Catamarca	GU360502	GU360478	GU359835	GU359430	GU359333
Eleusine indica (L.) Gaetrn.	Peterson 21362, Saarela & Flores Villegas (US)	Mexico, Mexico	GU360496	GU360472	GU359797	GU359473	GU359338
Enneapogon scaber Lehm.	Sachse 8 (MO)	South Africa, Western Cape	JQ345237	JQ345279	JQ345322	JQ345208	JQ345168
Entoplocamia aristulata (Hack. & Rendle) Stapf	Seydel 187 (US)	South Africa	GU360492	GU360468	GU359793	GU359469	GU359342
Eragrostiella leioptera (Stapf) Bor	Chand 7961 (US)	India	GU360529	JQ345280	GU359827	GU359486	GU359305
Eragrostis kennedyae F.Turner	Latz 13486 (MO)	Australia	JQ345238	JQ345281	JQ345323	JQ345209	JQ345169
Farrago racemosa Clayton	Peterson 23851, Soreng, Romaschenko & Abeid (US)	Tanzania, Lindi	KF827772	KF827706	KF827634	KF827582	KF827516
Gouinia brasiliensis (S. Moore) Swallen	Nee 36355 (US)	Bolivia, Sta. Cruz	–	KF827707	KF827635	–	KF827517
Gouinia gracilis Ekman ex Swallen	Ekman s.n. (US)	Cuba, Oricute	KF827773	KF827708	KF827636	–	KF827518

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Gouinia latifolia var. *guatemalensis* (Hack.) J.J. Ortíz	Beetle 918 (US)	Mexico, Yucatan	KX582969	KX582902	KF827637	KX582472	KF827519
Gouinia paraguayensis (Kuntze) Parodi	Peterson 11526 & Annable (US)	Argentina, San Juan	GU360504	GU360384	GU359817	GU359437	GU359314
Gouinia virgata var. *robusta* J.J. Ortíz	Reeder 4714 & Reeder (US)	Mexico, Zacatecas	KF827775	KF827710	KF827639	KF827584	KF827521
Gymnopogon ambiguus (Michx.) Britton, Sterns & Poggenb.	Thomas 168039 (BRY)	USA	KF827779	KF827716	KF827644	KF827587	KF827527
Gymnopogon aristiglumis Hitchc.	Calderon 949 (US)	El Salvador	KF827780	–	KF827645	–	KF827528
Gymnopogon brevifolius Trin.	Hill 15844 (US)	USA	KF827781	KF827717	KF827646	KF827588	KF827529
Gymnopogon burchellii (Munro ex Döll) Ekman	Swallen 8524 (US)	Brazil	–	–	KF827649	–	–
Gymnopogon chapmanianus Hitchc.	Anderson 19657 (US)	USA	KF827784	–	KF827650	–	–
Gymnopogon floridanus Swallen	Kral 51634 (US)	USA	–	–	KF827651	–	–
Gymnopogon grandiflorus Roseng., B.R. Arill. & Izag.	Peterson 16642 & Refulio-Rodriguez (US)	Peru, Apurimac	GU360581	GU360383	GU359816	GU359436	GU359200
Gymnopogon legrandii Roseng., B.R. Arrill. & Izag.	Carrasco 6293 (US)	Uruguay	KF827785	–	KF827653	–	KF827532
Gymnopogon spicatus (Spreng.) Kuntze	Quarin 4144, Urbani, Martinez & Kraemer (US)	Argentina	KF827786	KF827720	KF827654	KF827590	KF827533

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Gymnopogon swallenii J.P. Sm.	Irwin 8507 (US)	Brazil	KF827788	KF827721	KF827656	KF827591	KF827535
Hilaria cenchroides Kunth	Peterson 22339 & Saarela (US)	Mexico, Oaxaca	GU360697	GU360380	GU359813	GU359424	GU359143
Hilaria rigida (Thurb.) Benth. ex Scribn.	Boyd 11566 (BRY)	USA	JQ345269	JQ345311	JQ345356	JQ345229	JQ345200
Hubbardochloa gracilis Auquier	Troupin s.n. (MO)	Rwanda	–	–	–	–	KX582379
Leptocarydion vulpiastrum (De Not.) Stapf	Peterson 24238, Soreng & Romaschenko (US)	Tanzania	KF827792	KF827725	KF827660	KF827595	KF827539
Leptochloa digitata (R.Br.) Domin	Risler 476 & Kerrigan (MO)	Australia, Northern Territory	JQ345246	JQ345289	JQ345331	JQ345213	JQ345178
Leptothrium inermis (Chiov.) P.M. Peterson	Hemming 3416 (FT)	Somalia	KF827793	KF827726	KF827661	–	KF827540
Leptothrium rigidum Kunth	Davidse 3281 (MO)	Jamaica, Parish.	KF827794	KF827727	KF827662	KF827596	KF827541
Leptothrium senegalense (Kunth) Clayton	Peterson 24239, Soreng & Romaschenko (US)	Tanzania	KF827798	KF827731	KF827666	KF827599	KF827544
Lophacme digitata Stapf	Smook 1453 (MO)	South Africa, Transvaal	JQ345267	JQ345309	JQ345354	–	JQ345197
Monelytrum luederitzianum Hack.	Smook 10031 (US)	South Africa	GU360682	GU360421	GU359969	GU359459	GU359158
Mosdenia leptostachys (Ficalho & Hiern) Clayton	Schweickerdt 1542 (US)	South Africa	GU360681	GU360420	GU359967	GU359458	GU359159
Muhlenbergia schreberi J.F. Gmel.	Peterson 19443, Soreng, Salariato & Panizza (US)	Argentina, Tucuman	GU360679	GU360404	GU359950	GU359456	GU359161

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Neesiochloa barbata (Nees) Pilg.	Swallen 4491 (US)	Brazil	GU360724	GU360279	GU360005	–	GU359122
Neyraudia reynaudiana (Kunth) Keng ex Hitchcock	Soreng 5318, Peterson & Sun Hang (US)	China, Yunnan	–	GU360272	GU360003	GU359397	GU359124
Orinus kokonorica (K. S. Hao) Keng ex X. L. Yang	Soreng 5447, Peterson & Sun Hang (US)	China, Qinghai	GU360728	GU360270	GU359999	GU359399	GU359140
Pappophorum pappiferum (Lam.) Kuntze	Peterson 21689, Soreng, La Torre & Rojas Fox (US)	Peru, Ancash	GU360700	GU360276	GU359996	GU359402	GU359128
Perotis arenacea (Judz.) P.M. Peterson	Phillipson 4117 & Raharilala (MO)	Madagascar, Toliara	JQ345272	JQ345313	JQ345358	–	JQ345202
Perotis hildebrandtii Mez	Peterson 23814, Soreng & Romaschenko (US)	Tanzania	KF827799	KF827732	KF827667	KF827600	**MW241083**
Perotis hordeiformis Nees	Soreng 5717, Peterson & Sun Hang (US)	China, Sichuan	GU360708	GU360283	GU359991	GU359520	GU359132
Perotis indica (L.) Kuntze	Peterson 23880, Soreng & Romaschenko (US)	Tanzania	KF827801	KF827734	KF827669	KF827601	KF827546
Perotis leptopus Pilg.	Sheuyange & Lifo (US)	Namibia	KF827802	KF827735	KF827670	KF827602	KF827547
Perotis ornithocephala (Hook.) P.M. Peterson	Clayton 5582 (US)	Sri Lanka	GU360689	–	GU359878	–	–
Perotis patens Gand.	Godfrey 1661 (US)	South Africa	GU360707	GU360293	GU359990	GU359521	GU359133
Perotis rara R. Br.	Roc 1900 (US)	Australia	GU360706	GU360285	GU359989	–	GU359134
Perotis somalensis Chiov.	Clemmi 305 (FT)	Somalia, J. Hoose	–	–	KF827673	–	KF827550
Perotis vaginata Hack.	Reekmans 10368 (US)	Burundi	KF827805	KF827739	–	–	KF827551

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Schenckochloa barbata (Hack.) J.J. Ortíz	Swallen 4690 (US)	Brazil, Natal	KF827806	–	KF827674	–	KF827552
Sporobolus virginicus (L.) Kunth	Peterson 15683 & Soreng (US)	Chile, Region I	GU360610	GU360362	GU359892	GU359502	GU359215
Tetrachaete elionuroides Chiov.	Tardelli 254 (FT)	Somalia, Ghedo	–	–	**MW240441**	–	**MW241084**
Tragus berteronianus Schult.	FLSP 457 (US)	Peru	GU360616	GU360370	GU359898	GU359503	GU359224
Trichoneura elegans Swallen	Lundell 15030 (US)	USA, Texas	KF827807	KF827740	KF827675	KF827604	KF827553
Trichoneura eleusinoides (Rendle) Ekman	Seydel 448 (US)	South Africa	GU360705	GU360277	GU359988	GU359522	GU359135
Trichoneura grandiglumis (Nees) Ekman	Smook 7068 (US)	South Africa	KF827812	KF827745	KF827682	KF827610	KF827561
Trichoneura lindleyana (Kunth) Ekman	Bentley 319 (US)	Ecuador, Galapagos Islands	KF827813	KF827746	KF827683	KF827611	KF827562
Trichoneura mollis (Kunth) Ekman	Napper 550 (US)	Kenya, Lukenya	–	KF827748	KF827686	–	KF827565
Trichoneura weberbaueri Pilg.	Peterson 15686 & Soreng (US)	Chile	GU360668	GU360361	GU359948	GU359565	GU359172
Tridens flavus var. chapmanii (Small) Shinners	McCauley 438 (MO)	USA, Missouri	KF827817	KF827751	KF827689	KF827615	KF827568
Tridentopsis mutica (Torr.) P.M. Peterson	Peterson 21997& Saarela (US)	Mexico, Chihuahua	GU360667	GU360321	GU359947	GU359557	GU359173
Trigonochloa uniflora (Hochst. ex A. Rich.) P.M.P. & N.Snow	Snow 6978, Burgoyne & Gumbi (MO)	South Africa, Kwazulu Natal	–	–	JQ345348	–	JQ345192
Triodia intermedia Cheel	Peterson 14384, Soreng & Rosenberg (US)	Australia, Western Australia	GU360661	GU360327	GU359941	GU359563	GU359179

Taxon	Voucher	Country	*rps16-trnK*	*rps16* intron	*rpl32-trnL*	*ndhA* intron	ITS
Triplasis americana P. Beauv.	Kral 12065 (MO)	USA, Georgia	KF827818	KF827752	KF827690	KF827616	KJ768887
Triplasis purpurea (Walter) Chapm.	Peterson 14238, Weakley & LeBlond (US)	USA, North Carolina	GU360656	GU360347	GU359921	GU359536	GU359184
Tripogon multiflorus Miré & H.Gillet	Spellenberg 7441 (MO)	Yemen, Ibb Governorate	JQ345274	JQ345315	JQ345360	JQ345232	JQ345204
Triraphis mollis R. Br.	Peterson 14344, Soreng & Rosenberg (US)	Australia, Western Australia	GU360669	GU360336	GU359933	GU359539	GU359187
Tuctoria fragilis (Swallen) Reeder	Reeder 7255 & Reeder (US)	Mexico	–	–	GU359929	–	GU359189
Uniola condensata Hitchc.	Peterson 9342 & Judziewicz (US)	Ecuador, Chimborazo	GU360649	GU360340	GU359927	GU359534	GU359191
Vaseyochloa multinervosa (Vasey) Hitchc.	Swallen 10041 (US)	USA, Texas	GU360646	GU360342	GU359925	GU359544	GU359193
Zaqiqah mucronata (Forssk.) P.M. Peterson & Romasch.	Spellenberg 7470 (MO)	Yemen, Hodeidah Governorate	KX582977	KX582909	KX582663	KX582476	KX582387
Zoysia macrantha subsp. *walshii* M.E. Nightingale	Loch 435 (US)	Australia	GU360642	GU360345	GU359922	GU359548	GU359197

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PHORADENDRON LEUCARPUM SUBSP. *LEUCARPUM* (VISCACEAE) AT PERRYVILLE BATTLEFIELD STATE HISTORIC SITE, BOYLE COUNTY, KENTUCKY

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ABSTRACT

A survey for American mistletoe (*Phoradendron leucarpum* subsp. *leucarpum*) was conducted during 2006, 2015, 2016, and 2018 on 300-ha of the Perryville Battlefield State Historic Site (PBSHS) core battlefield area. Vegetation is of scattered mesophytic to subxeric deciduous woodlands among non-indigenous grasslands in rolling to steep hilly terrain of the Hills of the Bluegrass Ecoregion. A total of 102 mistletoe-infected host trees from eight facultative calciphilous tree species were documented: *Juglans nigra*, *Ulmus americana*, *Prunus serotina*, *Fraxinus americana*, *Celtis occidentalis*, *Robinia pseudoacacia*, *Maclura pomifera*, and *Acer saccharum*. Sixty-three mistletoe-infected trees were recorded within a 26-ha wooded grove of the PBSHS Museum and Visitor Center Headquarters and Interpretive Trail Markers 1–11. A significant determining factor for current scarcity of mistletoe at PBSHS includes the severe effects of extended mean minimum low winter temperatures of 2014–2015.

A preliminary field survey of American mistletoe [*Phoradendron leucarpum* (Rafinesque) Reveal & M.C. Johnston subsp. *leucarpum*] was made in 2006 to Perryville Battlefield State Historic Site (PBSHS) within the Hills of the Bluegrass Ecoregion of northwestern Boyle County, Kentucky. Mistletoe was vouchered from six host tree species within the wooded grove at the PBSHS Museum and Visitor Center Headquarters. This 2006 reconnaissance was the basis for a research survey of mistletoe-infected host trees in a 26-ha core battlefield area of the Museum and Visitor Center wooded grove and adjoining 274-ha PBSHS core battlefield area (Kentucky State Parks 2020) during 2015, 2016, and 2018. Our PBSHS study is a continuation of mistletoe surveys in east-central Kentucky to determine host tree specificity within the Inner Bluegrass, Hills of the Bluegrass, Outer Bluegrass, and Knobs-Norman Upland Ecoregions of Woods et al. (2002) and the effects of extended mean minimum low 2014–2014 winter temperatures on mistletoe.

Physical features of PBSHS

Perryville State Battlefield Site was established on October 8, 1954 (Noe 2001), and it was redesignated as Perryville Battlefield State Historic Site by the Kentucky Division of Parks on May 22, 1999, to preserve and protect the historic American Civil War site. In 1960, PBSHS was recognized as a National Historic Landmark (Noe 2001).

The 300-ha core battlefield area is a central tract within the total 580-ha of PBSHS land. The perimeter of the 580-ha area, counterclockwise, encompasses the Museum and Visitor Center (37.674362° -84.970594°) bordered by KY 1920 (Battlefield Road), north to KY 1331 (Whites Road),

west to KY 1314 (Hayes-May Road) south to Doctor's Fork Creek, south-southeast to KY 1920, and back north to the Museum and Visitor Center entrance (Kentucky State Parks 2020). Elevations range from 270 m above sea level at the Museum and Visitor Center to 285 m at the Russell House down to 247 m at Doctor's Fork Creek where it empties into the Chaplin River (Cressman 1974).

Perryville Battlefield State Historic Site is situated in the Interior Low Plateau Physiographic Province entirely within the Hills of the Bluegrass (Woods et al. 2002), or Eden Shale Hills (Campbell 2003). Geology of the Hills of the Bluegrass is composed of Upper Ordovician calcareous shale, siltstone, and limestone. Holocene shale, limestone cobbles, and aggregate alluvium occur along major streams (Carey et al. 2006). Bedrock at PBSHS consists of Garrard Siltstone and Clays Ferry Limestone, Middle and Upper Ordovician shale, siltstone, and Lexington limestone with shale, siltstone, and limestone surface outcrops (Cressman 1974; Carey et al. 2006).

Upland residual soils are an intermixed mosaic of 11 soil units in the PBSHS area (Craddock 1983; Soil Survey Staff 2019). Eden, Lowell-Faywood-Eden, and Eden-Lowell soil associations are acid to moderately alkaline, well-drained, deep soils on gently rolling to steep hilly terrain underlain by weathered shale, siltstone, and limestone, or just limestone (Craddock 1983). These three soil associations comprise the majority of the PBSHS uplands (Soil Survey Staff 2019). Caleast-McAflee-Maury soil series are slightly acid to mildly alkaline, well-drained, deep to shallow soils, on level to steep hills underlain by limestone or limestone surface outcrops. Newark-Nolin series are deep, poorly to well-drained, slightly acid to neutral silt loams on alluvial floodplains along intermittent creeks and Doctor's Fork (Craddock 1983).

Braun (1950) described forest vegetation of the broad Interior Low Plateau Province as Western Mesophytic Forest, a mosaic of eastern Oak-Hickory (*Quercus-Carya*) Forest and Mixed Mesophytic Forest. The deciduous forest land-cover classes of the Hills of the Bluegrass are largely restricted to scattered woodlands and woodlots of Oak-Ash-Elm (*Quercus-Fraxinus-Ulmus*) Forest with upland terrain dominated by large tracts of disturbed non-indigenous grassland for crops, hay, and pasture (Campbell 1987). Woods et al. (2002) described vegetation of the Hills of the Bluegrass Ecoregion as mixed Oak-Hickory-Ash (*Quercus-Carya-Fraxinus*) Forest on mesic terrain with Oak-Hickory-Red Cedar (*Quercus-Carya-Juniperus*) stands on subxeric hilly terrain.

American mistletoe biology

Using the name established by Reveal & Johnston (1989) for American mistletoe, *Phoradendron leucarpum*, and accepting entities and taxonomic ranks of Kuijt (2003), Abbott and Thompson (2011) provided a new set of subspecies combinations for *P. leucarpum*. Weakley (2020) follows this nomenclature.

Phoradendron leucarpum subsp. *leucarpum* is the only subspecies native to the eastern USA. The distribution of American mistletoe, clockwise, is eastern Texas and Oklahoma, Arkansas, southern Missouri, Tennessee, and Kentucky, north alongside the Ohio River of southern Illinois, Indiana, Ohio, to West Virginia, east to Maryland and Delaware and southward throughout the Mid-Atlantic and Gulf Coastal States back to Texas (Kuijt 2003; Mallams & Mathiasen 2010). American mistletoe is a southern intraneous geographical species primarily within the southern USA distribution (Thompson & Jones 2001). Mistletoe extends more than 160 km north of PBSHS in east-central Kentucky.

Eastern USA host tree studies

Kuijt (2003) reported 77 mistletoe host tree species for the eastern USA from herbarium specimen data. Overlease and Overlease (2005) recorded 41 host tree species in an extensive mistletoe field study of the distribution, abundance, and host species in the eastern USA.

Kentucky mistletoe studies

Reed and Reed (1951) listed 24 host trees for 76 Kentucky counties from American mistletoe observations and specimen collections. Statewide, the five mistletoe-infected hosts they observed in decreasing order of occurrence were black walnut (*Juglans nigra*), blackgum (*Nyssa sylvatica*), American elm (*Ulmus americana*), black locust (*Robinia pseudoacacia*), and honey locust (*Gleditsia triacanthos*). Overlease and Overlease (2005) observed 16 host tree species among 557 host trees in Kentucky. They reported black walnut comprised 44% of the total followed by silver maple (*Acer saccharinum*), American elm, black locust, black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), hackberry (*Celtis occidentalis*), sugar maple (*Acer saccharum*), and Osage-orange (*Maclura pomifera*).

Braun (1943) stated mistletoe was widely distributed in Kentucky and listed 32 counties among several host trees. Wharton and Barbour (1973) reported mistletoe in Kentucky on black walnut, American elm, hackberry, black locust, honey locust, and other trees. Campbell et al. (2020) mapped 119/120 Kentucky counties based on R.L. Thompson's vouchers from his statewide survey of American mistletoe.

Kentucky Bluegrass mistletoe studies

Wharton and Barbour (1991) referred to the "Kentucky Bluegrass" as the total area of Ordovician outcrops within the Inner Bluegrass, Hills of the Bluegrass, and Outer Bluegrass Physiographic Regions. Braun (1943) reported mistletoe was especially abundant in the Bluegrass Region (Inner Bluegrass, Hills of the Bluegrass, Outer Bluegrass) on several hardwood tree species. Coulter (1877) observed American elm and black walnut as the dominant mistletoe-infected trees in Louisville, Jefferson County, in the Outer Bluegrass. Willis (1873) noted mistletoe in Bourbon County in the Inner Bluegrass on Ohio buckeye (*Aesculus glabra*), honey locust, bur oak (*Quercus macrocarpa*), and black locust. Schneck (1884) found mistletoe to be common on black walnut and black cherry in the Kentucky Bluegrass Region. Garman (1913) reported black walnut as the most common mistletoe host in the Kentucky Bluegrass followed by black locust and American elm. In the Ordovician Kentucky Bluegrass, Reed and Reed (1951) observed the principal mistletoe-infected hosts were black walnut followed by American elm, black locust, honey locust, hackberry, maples (*Acer* spp.), Osage-orange, white ash, and black cherry in descending order. Within the Inner Bluegrass ecoregion, Wharton and Barbour (1991) stated mistletoe was present on several tree species with black walnut the most common and elms (*Ulmus* spp.) and hackberry occasionally infected.

Eight American mistletoe surveys have been published from 1992–2010 within the Inner Bluegrass, Hills of the Bluegrass, Outer Bluegrass, Knobs-Norman Uplands, and Eastern Highland Rim ecoregions of Woods et al. (2002). A total of 33 mistletoe host woody plants have been documented (31 trees, a shrub, a vine) in those mistletoe surveys (Thompson 1992; Thompson & Noe, Jr. 2003; Thompson 2005; Thompson & Poindexter 2005; Thompson et al. 2008; Taylor & Thompson 2009; Thompson & Rivers Thompson 2009; Thompson & Evans 2010).

METHODS

We conducted our survey of *Phoradendron leucarpum* subsp. *leucarpum* in fall of 2006 and the winter and spring of 2015, 2016, and 2018 within the 300-ha PBSHS core battlefield area. Nikon Monarch (8 x 25 power) binoculars were used to identify signs of mistletoe infestation on infected host trees, e.g., branch cankers or swellings, stem clumps, clusters, brooms, shoots, and limb die-back. Each host tree was scored according to a Mistletoe Infestation Scale (MIS) from external obvious signs (Thompson et al. 2008; Thompson 2014): light-infestation (1–10 clusters), moderate-infestation (11–30), heavy-infestation (31–100), and extensive-infestation (>101). Mistletoe *infestations* are external visible signs to an internal *infection* response in host trees.

Mistletoe vouchers with host tree twigs were gathered from 25 different infected trees with a 12 m extendible fiberglass linesman pole. At the PBSHS Headquarters wooded grove, 21 mistletoe vouchers were collected from eight representative trees from one to four times to observe infestation and freeze data effects. Specimens were dried, mounted, labeled, and deposited in the Berea College Herbarium (BEREA). Tree nomenclature follows Jones (2005).

RESULTS AND DISCUSSION

We observed 102 mistletoe-infected host trees from eight facultative calciphilous species at PBSHS (Table 1). Black walnut accounted for over 41% of the host trees with the following in descending order of occurrence: American elm, black cherry, white ash, hackberry, black locust, Osage-orange, and sugar maple (Table 1). Sixty-three (61.76%) of 102 mistletoe-infected trees were documented within a 26-ha wooded grove of the PBSHS Museum and Visitor Center Headquarters, and Interpretive Markers 1–11 (Table 1).

In previous articles involving mistletoe from Boyle County, Garman (1913) reported mistletoe on black walnut among several other counties, Reed and Reed (1951) observed black walnut, Osage-orange, black locust, and American elm as host trees, and Braunrieter (2015) collected mistletoe without designating a host tree species.

Table 1. *Phoradendron leucarpum* host occurrence at Perryville Battlefield State Historic Site (2018).

Host Trees	HQ*	Areas**	Trees	Clumps	% Trees
Juglans nigra L	19	23	42	472	41.18
Ulmus americana L.	12	4	16	194	14.71
Prunus serotina Ehrh.	10	4	14	28	13.73
Fraxinus americana Marsh.	10	1	11	41	10.78
Celtis occidentalis L.	7	3	10	57	9.80
Robinia pseudoacacia L.	1	4	5	7	4.90
Maclura pomifera (Raf.) Schneid.	3	1	4	13	3.72
Acer saccharum Marsh.	1	0	1	5	0.98
Total Species = 8	63	39	102	817	100.00

*HQ=PBSHS Headquarters wooded grove (26-ha.)
**Areas=Other PBSHS lands (474-ha.).

In the following six east-central Kentucky mistletoe studies, we followed delineation for the "Kentucky Bluegrass" (Wharton & Barbour 1991) as comprising the Inner Bluegrass, Hills of the Bluegrass, Outer Bluegrass, and the Knobs-Norman Uplands of Woods et al. (2002). These six mistletoe studies include the survey at PBSHS (Table 2) among the dominant host tree sp ecies in respective order of occurrence, percentage, and Woods et al. (2002) ecoregion(s).

The most common host trees in all six mistletoe surveys were *Juglans nigra* (JUNI), *Ulmus americana* (ULAM), and *Prunus serotina* (PRSE), although the overall order of host tree incidence varied with the particular ecosystems; geological substrate, soils, vegetation, tree dominance or codominance, and area size, among other variables (Table 2). In east-central Kentucky mistletoe surveys, the same eight host tree species at PBSHS were among those documented for Garrard County (Thompson & Poindexter 2005); city of Berea (Thompson et al. 2008); Jessamine County (Thompson & Evans 2010), and seven of eight hosts at the Lexington-Blue Grass Army Depot (Thompson 1992).

Table 2. Six east-central Kentucky *Phoradendron leucarpum* host occurrence studies.

County & Site	Tree Species	Total Trees	Major Hosts*	%	Ecosystem(s)**
Boyle Co. PBSHS Thompson et al. (2020)	8	102	JUNI, ULAM, PRSE	70.36	HB
Robertson Co. Thompson (2005)	7	45	JUNI, ULAM	73.30	HB
Jessamine Co. Thompson & Evans (2010)	10	1403	JUNI, PRSE, ULAM	89.10	IB
Garrard Co. Thompson & Poindexter (2005)	12	1740	JUNI, PRSE, ULAM	80.46	IB, HB, OB, KN
Madison Co. LBGAD Thompson (1992)	14	1837	PRSE, JUNI, ULAM	86.76	OB
Madison Co. Berea Thompson et al. (2008)	22	2320	PRSE, JUNI, ULAM	70.64	OB, KN

*Tree Codes: JUNI=*Juglans nigra*; PRSE=*Prunus serotina*; ULAM=*Ulmus americana*.
**Ecosystems: IB=Inner Bluegrass; HB=Hills of the Bluegrass; OB=Outer Bluegrass; KN=Knobs-Norman Uplands (Woods et al. 2002).

PBSHS mistletoe infestation dynamics

The four ecoregions of east-central Kentucky (Inner Bluegrass, Hills of the Bluegrass, Outer Bluegrass, and Knobs-Norman Uplands) have associated and comparable features in geology, topography, substrate-derived soils, existing mesophytic forest, and culturally disturbed vegetation (Woods et al. 2002). Most of the infected hardwood host trees are facultative calciphilous (calcicolous) in these ecoregions. Calcicolous host trees thrive best in predominantly alkaline calcareous medium or limestone-based soils (Reed & Reed 1951; Thompson & Rivers Thompson 2009; Thompson & Evans 2010).

At PBSHS, as in previous studies, most mistletoe-infected trees were older, taller and typically with full canopy crowns and in wooded groves, or solitary and scattered trees of open upland habitats, e.g., fence rows, fields, pastures (Thompson 1992; Thompson & Noe, Jr. 2003; Thompson & Poindexter 2005; Thompson & Evans 2010). Frugivorous birds congregate or flock among the largely open wooded grove at the PBSHS Museum and Visitor Center Headquarter, not unlike other surveys of avian allurement for mature host trees in towns and small cities, to feed, perch, and roost (Thompson & Noe, Jr. 2003; Thompson & Poindexter 2005; Thompson et al. 2008).

The Mistletoe Infestation Scale was recorded for the eight host trees selected from the wooded grove at PBSHS Museum and Visitors Center Headquarters (Table 3). A total of 21 representative annotated voucher specimens were collected from these eight host trees.

Our American mistletoe study at PBSHS reports consequences of two severe cold winters, 2014 and 2015, over a 12-year period (2006–2018). Observations and one to four mistletoe specimens were collected from the same eight host tree species (Table 3). A *Juglans nigra* changed from heavy-infestation (*06-749*; *15-34*; *16-14*) to extensive-infestation (*18-353*) approaching mortality from 2006 to 2018. Black walnut was the major infected tree with the most visible signs (Tables 1, 3). An *Ulmus americana* scored moderate (*06-333; 15-38; 16-07*) to heavy-infestation (*18-354*) over the same period. American elm was the second most infected tree with visible signs from light to heavy infestation (Tables 1, 3). The *Prunus serotina* exhibited light-infestation (*06-754*; *15-33*; *16-13*) with an increase of new clusters (*18-355*), while the other black cherries at PBSHS had few clumps or one or two cankers. An old mature *Fraxinus americana* exhibited only light-infestation (*06-752, 15-39*) with large gnarled, clavate swellings. Shoot and limb die-

back were evident in all 11 white ashes observed (Tables 1, 3). Hackberry had light-infestation (*06-733; 15-36; 18-356*) in all 10 hackberries at PBSHS. A single black locust showed light-infestation with one large branch canker (*06-750*) and mistletoe never recovered from winter freezes. Four of the five black locust at PBSHS contained only one or two clumps for eight total (Tables 1, 3). An Osage-orange had light-infestation with four clumps (*15-35*) and added a new cluster (*18-355*). Four infected Osage-orange trees possessed a total of 13 clumps. The tall mature sugar maple had only light-infestation (*15-42*) with five branch clumps (Tables 1, 3).

Table 3. Eight host tree species at PBSHS Museum Headquarters wooded grove in sequence by species, MIS infestation values, dates, collector's initials and numbers.

Standard Label Data: BOYLE COUNTY: *Phoradendron leucarpum* (Raf.) Rev. & M.C. Johnst. subsp. *leucarpum.* Perryville Battlefield State Historic Site (PBSHS), 1825 Battlefield Road (KY 1920), Museum and Visitors Center, and Monument Headquarters. Elev. 265–272 m, ca. 37.674557°, -84.970594°: Hemiparasitic on:

1 *Juglans nigra*, ~15 m tall tree, heavy-infestation, ~60–70 clumps and cankers, 29 Oct 2006, *RT & KR 06-751*; ~40+ clumps, clusters, limb cankers, 13 Apr 2015, *RT & CT 15-34*; heavy-infestation, 70–80 clumps, cankers, limb die-back, 17 Mar 2016, *RT & ND 16-14*; extensive-infestation trending toward tree mortality due to infection, >100+ clumps, gnarled limb cankers, branch die-back, 1 Dec 2018, *RT & ND 18-353.*

2 *Ulmus americana*, ~14 m tree, moderate-infestation, ~35–40 small clusters, 29 Oct 2006, *RT & KR 06-749*; 20–25 scattered clumps, 13 Apr 2015, *RT & CT 15-38*; heavy-infestation, ~35–40 clumps, 17 Mar 2016, *RT & ND 16-07*; ~15 m tree, ~60–70 clusters scattered on limbs and trunk, 1 Dec 2018, *RT & ND 18-354*.

3 *Prunus serotina*, ~9–10 m tall, light-infestation, 2 small clusters on one of five black cherries planted in a row infected, 29 Oct 2006, *RT & KR 06-754;* 2 clusters, 13 Apr 2015, *RT& CT 15-33*; 3 small clusters, 17 Mar 2016, *RT & ND 16-13*; 4–6 new growth clumps and three more cherries infected, 1 Dec 2018, *RT & ND 18-355.*

4 *Fraxinus americana*, ~17–18 m tall, light-infestation, 6–7 clavate, knobby cankers and sparse old broom shoots, in an old ash among other infected white ashes, 29 Oct 2006, *RT & KR 06-752*. 3–4 severe old clavate cankers and broom shoot dieback, no new shoots, 13 Apr 2015, *RT & CT 15-39*.

5 *Celtis occidentalis*, ~12 m tall, light-infestation, 3–5 clumps; three other infected hackberry in a row, 29 Oct 2006, *RT & KR 06-753;* 2–4 clumps, 13 Apr 2015, *RT & CT 15-36*; 6–7 small clusters, 1 Dec 2018, *RT & ND 18-356.*

6 *Robinia pseudoacacia*, ~16 m tall, light-infestation, one large limb canker and broom shoots; broom shoots shattered after 2015 freezes, not recollected, 29 Oct 2006, *RT & KR 06-750.*

7 *Maclura pomifera*, ~15 m tall, light-infestation, 3–4 large clumps; two additional Osage-orange trees infected, 13 Apr 2015, *RT & CT 15-35*; 5–6 clumps, a new limb cluster collected, 1 Dec 2018, *RT & ND 18-357*.

8 *Acer saccharum*, ~18–19 m tall, light-infestation, 5 small clumps at top of sugar maple; no additional new signs evident, not recollected, 13 Apr 2015, *RT & CT 15-42*.

Collector's initials: RT=Ralph L. Thompson; KR=Katrina Rivers Thompson; CT=Craig A. Thivierge; ND=Gary Neil Douglas.

The incidence of mistletoe-infected trees tended to be in close proximity to other host trees at the PBSHS Headquarters wooded grove. This aggregated (clumped) spatial distribution likely results from ornithophily (Thompson & Noe, Jr. 2003; Thompson & Poindexter 2005; Gougherty 2013; Thompson 2014). Coder (2008) noted variable incidence of mistletoe in forested communities was due in part to the availability of host trees and attributes of bird behavior for dispersal, establishment, and spread.

Low winter temperature and duration factors

The duration of low winter temperature has been reported as the major factor influencing the incidence, abundance, and northern distribution of American mistletoe in the eastern USA (Spooner 1983; Coder 2008). Medley (1993) listed mistletoe as hemiparasitic on a large number of trees throughout Kentucky with rare to common abundance based on cyclic severity of winters. Clark and Weckman (2008) reported mistletoe throughout Kentucky with incidence very common southward but increasingly rare northward.

Spooner (1983) reported that mistletoe reaches its northern distribution limits in southern Ohio and produced evidence the main reason for the northern limits of mistletoe corresponded to the mean minimum January temperature of -4.5° C. Coder (2008) stated the minimum December daily temperature of -3.9° C was the limiting factor in the northern range of American mistletoe, while the western expansion of American mistletoe was restricted by 63.5 cm annual precipitation.

Several American mistletoe studies in the USA document effects of low winter temperature and its duration on the prevalence, external mistletoe death, and eventual endophyte recovery with range increases during warmer temperatures: Illinois (Schneck 1884; Fuller 1955; Thompson 2014); Indiana (Deam 1932); Kentucky (Coulter 1877; Garman 1913; Shacklette 1937; Thompson 2005; Thompson et al. 2008); Ohio (Braun 1961; Spooner 1983); and, Oklahoma (Gould 1901). Other studies of *Phoradendron* spp. on low winter temperature effects, duration, and distribution and have been recorded for Arizona and New Mexico (Bray 1910; Lightle et al. 1964) and California (Bray 1910; Wagener 1957).

Boyle County and most of Kentucky is located within the 6b (-17.8° C to -20.6° C) USDA Plant Hardiness Zone Map (USDA, ARS 2012). Recent extended 2014 and 2015 low mean minimum temperatures duration in days through January, February, and March 2014–2015 (Table 4), were a primary limiting factor for the scarcity of mistletoe at PBSHS. The 2014–2015 low mean minimum temperatures at PBSHS (Table 4) were comparable to the low temperatures of mistletoe survival recorded for other *Phoradendron* spp. survival studies (Wagener 1957; Lightle et al. 1964), and the Plant Hardiness Zone Map for Kentucky (USDA, ARS 2012).

Table 4. Minimum, mean minimum, and days at minimum (° C) in Marion Co., Kentucky* (Midwest Regional Climate Center 2020).

Year	Time Period	Minimum	Mean Minimum	Days at Minimum
	1/02–1/09	-20.0	-15.1	3
	1/21–1/31	-21.1	-16.0	4
2014	2/05–2/18	-14.4	-8.6	2
	2/24–3/06	-10.0	-8.0	4
2014--2015	12/30–1/03	-7.8	-6.9	2
	1/05–1/21	-17.2	-8.7	4
	1/27–2/07	-11.1	-7.0	10
2015	2/11–2/21	-27.8	-15.7	2
	2/23–3/03	-12.8	-9.8	2
	3/05–3/08	-21.1	-19.6	3
	3/28–3/30	-6.7	-6.5	3

*Marion County, is the closest weather station to Boyle County with a contiguous eastern border.

Dead and dying external mistletoe signs (brittle leaves, stems, and shoots) fragmented and sloughed off after January, February, and March of 2014 and especially during 2015. The mistletoe internal endophyte haustoria system produced new mistletoe growth during 2016–2018 in the majority of host trees. Conversely, new mistletoe signs did not reappear in a few trees, e.g., a white ash (*15-36*), a black cherry (*16-43*), a black locust (*06-750*), and an American elm (*16-15*).

American mistletoe is sparse and rarely present in the northern Kentucky counties. Mistletoe distribution in the Ohio River Valley typically follows the -4.5° C mean January isotherm mapped by Spooner (1983). The 6a (-20.6° C to -23.3° C) USDA Plant Hardiness Zone Map covers those areas where mistletoe terminates in the southern parts of the states north of the Ohio River (Spooner 1983; Mallams & Mathiasen 2010; Thompson 2014).

Schneck (1844) recorded -17.8° C as a critical temperature for survival of *Phoradendron leucarpum* at Mt. Carmel, Illinois. Thompson (2005) noted the low January 1996 temperature of -22.1° C caused extensive mistletoe die-back in Robertson County, Kentucky. In northern California, Wagener (1954) reported low minimum temperatures below -17.8°C over a seven day period from -18.8° C to -25.5° C (*m*= -19.5° C), killed all external and endophyte systems in dense mistletoe (*Phoradendron densum* Torrey ex Trelease). Comparably, Lightle et al. (1964) reported a low temperature range of -12.7° C to -18.8° C (*m*= -15.3° C) at seven stations over a two-day period caused severe cold injury to mesquite mistletoe (*Phoradendron californicum* Nuttall) in southern Arizona. Based partly on Table 4 data, the mean January isotherm map of the Ohio River Valley (Spooner 1983), and the 6b zone (-17.8° C and -20.6° C), mean annual minimum temperature of the USDA Plant Hardiness Zone Map (USDA, ARS 2012), the critical minimum low temperature of American mistletoe severe injury or death in Kentucky may be estimated at -18.0° C to -21.0° C, or lower.

American mistletoe in east-central Kentucky is well within its natural geographical range. The northern range is limited to the Ohio River Valley (Braun 1961; Spooner 1983). Mild winter temperatures during 2016–2020 (Midwest Regional Climate Center 2020) within the 6b Plant Hardiness Zone have been advantageous to American mistletoe establishment, growth, and proliferation in most host trees at Perryville Battlefield State Historic Site and throughout Kentucky.

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LIFE IS ROUGH: *PETREA ASPERA* AND *P. ASPERIFOLIA* (VERBENACEAE), THE FIRST AN OLD, GOOD SPECIES, NEWLY RECOVERED FROM SYNONYMY AND NEWLY REPORTED FOR COSTA RICA, THE SECOND A NEW COMBINATION

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ABSTRACT

The species treated as "*Petrea* sp. 1" in the recently published Vol. VIII of the *Manual de Plantas de Costa Rica* already has a name, **Petrea aspera** Turcz., here recovered from synonymy of *P. volubilis*. Because the new name *Petrea xolocotzia* for the transfer of *Xolocotzia asperifolia* to *Petrea* was unnecessary, the new combination **Petrea asperifolia** (Miranda) Hammel, **comb. nov**., is here presented.

RESUMEN

La especie tratada como "*Petrea* sp. 1" en el recientemente publicado Vol. VIII del *Manual de Plantas de Costa Rica* ya tiene un nombre, **Petrea aspera** Turcz., aquí sacado de la sinonimia de *P. volubilis*. Dado que el nombre nuevo *Petrea xolocotzia* para la transferencia de *Xolocotzia asperifolia* a *Petrea* no fue necesario, la combinación nueva **Petrea asperifolia** (Miranda) Hammel, **comb. nov**., se presenta aquí.

In preparing this manuscript to publish a name for "*Petrea* sp. 1" from the *Manual de Plantas de Costa Rica* (Rueda & Hammel 2015) we looked, somewhat belatedly, at Moldenke's treatment for the Flora of Panama (1973). There we found a perfectly good, old name for it, *Petrea aspera* Turcz. Confession: although Rueda was first author of the *Petrea* treatment for the Manual, by mutual agreement with the second author, he had little to do with the taxonomic decision to recognize *P.* sp. 1 distinct from *P. volubilis* L. By the same token, we take full blame for the taxonomy here presented. Flashback and update: Rueda (1994) reduced the number of extant, species of *Petrea* from ca. 32 (accepted by Moldenke, the previous monographer of the genus) to just 11, all restricted to the New World tropics. Sixteen of the new synonyms—including *P. aspera*—were subsumed under *P. volubilis* alone. No new species have been described subsequent to Rueda's revision. However, the recent transfer (Christenhusz & Byng 2018) of monospecific *Xolocotzia* (either sister to or nested within *Petrea*; Marx et al. 2010) to *Petrea* adds one more (see note below). And now, this exhumation of *P. aspera* brings the total count to 13 species. We present the following in a format similar to that for a new species in order to distinguish *P. aspera* clearly and advocate for its reconsideration as a distinct species.

PETREA ASPERA Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(3–4): 211. 1863. **LECTOTYPE** (designated by Rueda, Novon 3: 179. 1993): **VENEZUELA. Carabobo**. Near San Estevan, 300 m elev., Apr–May 1845–1846, *Funck & Schlim 507* (BR-photos at F, MO, NY(2), TEX, U, W; isolectotypes: BM, G-2 sheets).

Figure 1. *Petrea aspera*. A. Habit. B, C. Fruiting calyx. D, E. Fruiting calyx of *P. volubilis*. A-C from *Aguilar 3209*; D, E from *Fuentes 291*.

Similar to the Panamanian and South American *Petrea blanchetiana* in its smooth to subscabrous leaves and lack of glandular trichomes on the calyx tube, but differing from it principally by its axillary (vs., mostly terminal) inflorescences and flowers with a shorter pedicel and smaller corolla. Differing, at least in Costa Rica, from the sympatric, widespread and also with axillary inflorescences *P. volubilis* (with markedly scabrous leaves and glandular pubescent calyx tube) not only by those two characters, but also by the shape of its calyx lobes (elliptic to narrowly spatulate with the sinus between adjacent lobes open, vs oblong with the sinus closed) and size (in fruit) of the lobes of the calycine crest 2.5–3.5 (vs 1–1.5) mm.

Liana climbing to at least 15 m, the stem up to ca. 10 cm in diameter; the branchlets terete to obtusely tetragonal flattened, puberulent to glabrescent. **Leaves** with the petiole 0.5–1 cm, glabrate or subpuberulent, glabrescent; blade 7–25 × 4–9(–11) cm, elliptic to lanceolate, the base obtuse to acute, the apex obtuse to acuminate, smooth to the touch or slightly asperous on both surfaces, glabrate on both surfaces. **Inflorescences** axillary, racemiform, 9–39 × 5–8 cm. **Flowers** with the pedicel 5–11 mm, glabrous, the bracteoles 3.5–4.8 mm, early deciduous (gone by the time the corolla opens); calyx lavender, the tube ca. 4.8 mm, obconic, corrugated, sparsely and minutely substrigulose, without glandular trichomes, 5-lobed, the sinuses open, the lobes, (8–)15–21(–25 in fruit) mm, elliptic to narrowly spatulate, the apex obtuse to acute, glabrous; calycine crest with the lobes 2–2.4 mm, the apex obtuse to acute, glabrate o glabrous; corolla lavender to dark lavender, the tube 6.7–8 mm, the lobes 5, 5–8 mm, puberulent, the largest lobe with a white spot adaxially at the base, the remaining lobes slightly smaller and lavender throughout; stamens with the filaments ca. 2 mm long, sparsely pilose; anthers ca. 1.5 mm long and 0.5 mm wide; ovary oblong, glabrous; style 2.5 mm long, glabrous; stigma subcapitate. **Fruits** with the sinuses of the calyx lobes open, the calycine crest with the lobes 2.5–3.5 mm. Figure 1.

Phenology (in Costa Rica), habitat, and distribution. Flowering Feb, Apr–Jun. Climbing on vegetation, often near water 0–200 (–650, cult.) m. In Costa Rica, wild only on the Pacific slope (Puntarenas), Golfo Dulce region, especially Osa Peninsula, also cultivated on the Caribbean slope (Cartago), vicinity of Turrialba. Known overall from Costa Rica, Panama, Colombia, Venezuela, French Guiana, and Brazil.

Specimens examined. **COSTA RICA**. **Cartago**. Cantón de Turrialba, Instituto Interamericano De Ciencias Agricolas (cult.), 17 Feb 1968 (fr), *Córdoba 833* (CR); CATIE (cult.), 15 Jun 1977 (fl), *Poveda y Albertín 1647* (CR). **Puntarenas**. Cantón de Osa, Dist. Palmar, 2-3 km NW de Chacarita, bosques poco o nada alterados a la orilla de la Carretera Interamericana, 3 Feb 1994 (fl), *Hammel et al. 19417* (CR); Dist. Sierpe, península de Osa, Aguabuena, 14 Apr 1994 (fr), *Aguilar 3209* (CR, MO); borde del manglar entre Rincón y puente sobre el Río Rincón, 1 May 2020 (fl), *Aguilar 17367* (CR); P.N. Corcovado, on mirador trail near Río Sirena, 19 Feb 1988 (fl), *Kernan 203* (CR); Cantón de Golfito, Dist. Jiménez, Parque Nacional Corcovado, Estación El Tigre, Rio Tigre, Fila Rompepecho, 2 May 1997 (fl), *Azofeifa 299*, (CR, MO).

Representative images examined. **PANAMA**. **Veraguas**. San Francisco, Feb 1924 (fl.), *Powell s.n.* (US #1206763, Barcode: 03203037). **Panama.** Forests along Río Boquerón above Peluca Hydrographic Station, 22 Feb 1935 (fl.) *Hunter & Allen 658* (US). **Darien**. Río Sambu between Sambú y Río Venado 18 Jan 1967 (fl.) *Duke 9303* (US). **COLOMBIA**. **Antioquia**. Along river above Chigorodo, 40 km. S of Turbo, 16 Apr 1945 (fl.) *Haught 4569* (US). **Santander**. Vicinity of Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado rivers, 19 Feb 1935 (fl.), *Haught 1568* (US). **VENEZUELA**. **Carabobo**. Apr–May 1845–1846 (fl.), *Funck & Schlim 507* (BM, BR, G, LD, KM, KW, P). **Delta Amacuro**. Serrania Imataca, El Palmar-Raudal Trail, upper Río Toro drainage, 10 Nov 1955 (fl.) *Wurdack & Monachino 39641* (US). **BRAZIL**. **Mattogrosso**. Dec 1914 (fl.) *Kuhlmann 1296* (NY).

Etymology. One can only wonder why Turczaninow chose the epithet “aspera” for a species in his own words described as having exasperate leaves. Perhaps the epithet relates to the stems,

which he described as asperate. In fact the leaves of the present species can be slightly asperous, but never as strongly so as those of *P. volubilis*.

Petrea aspera is known from the wild in Costa Rica only from the Pacific slope, in the Golfo Dulce region where the otherwise more common *P. volubilis* is apparently known only from cultivation. Of *P. aspera* we have seen only two specimens from cultivated plants, both of them from the Atlantic slope, from the same campus in Turrialba, Cartago. *Petrea volubilis*, on the other hand, is commonly cultivated as an ornamental, but it is also more widespread in the wild. From the Golfo Dulce region on into adjacent Panama, *P. aspera* is by far the more commonly collected species. All but one (*Colwell 374*) of the 18 images currently det. to *P. volubilis* at US (https://collections.nmnh.si.edu/search/botany/?ti=3) were originally det. to *P. aspera* by Moldenke and (when fertile) we confirm them as fitting the concept of the latter as presented here. As indicated in the Manual, *P. aspera* (as *P.* sp. 1) differs from the only other Costa Rican species *P. volubilis* by its smooth to subscabrous (vs. notably scabrous) leaves that are glabrate on both surfaces (vs sparsely to densely pilose on the lower surface) and its glabrate (minutely and sparsely substrigose) calyx tube that lacks glandular trichomes (vs densely hirsute with numerous glandular trichomes). For the first and last of these features, *P. aspera* resembles *Petrea blanchetiana* (=*P. morii* Moldenke) from Panama, Colombia and Peru, Venezuela, French Guiana and Brazil. It differs from that species principally by its axillary (vs., terminal) inflorescences and flowers with a shorter pedicel (5–11 vs 10–31 mm) and smaller corolla (the tube 6.7–8 vs 13–22 mm. In Costa Rica *Petrea aspera* also differs consistently from *P. volubilis* in the shape of its calyx lobes (elliptic to narrowly spatulate with the sinus between adjacent lobes open, vs oblong with the sinus closed) and size (in fruit) of the lobes of the calycine crest 2.5–3.5 (vs 1–1.5) mm. Figures 2–4.

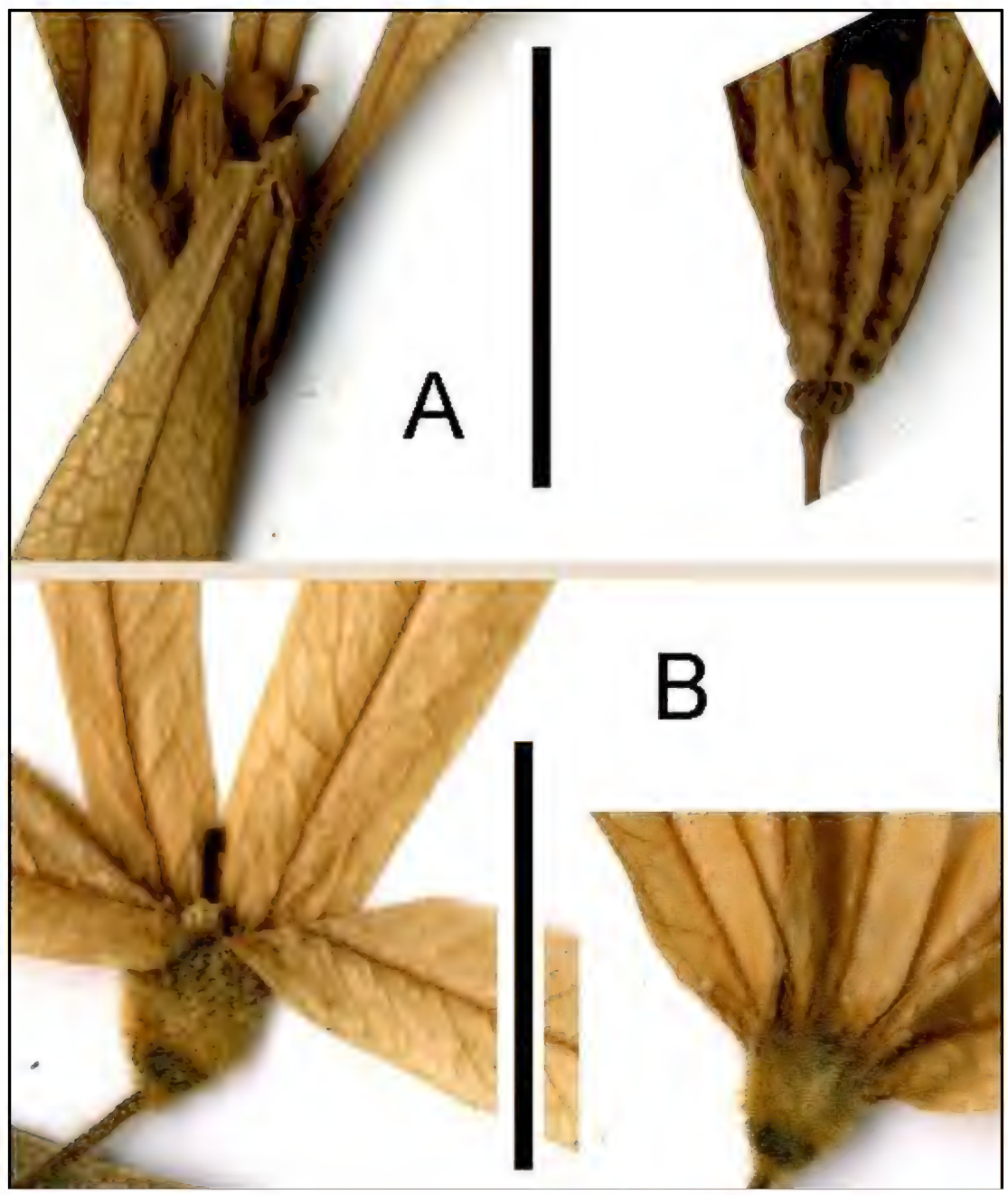

Figure 2. Details at of base of fruiting calyx. A. *Petrea aspera*. B. *Petrea volubilis.* A from *Aguilar 3209*, B from *Fuentes 291*. Scale bars = 10 mm.

Figure 3. Comparison of live material. A, B, *P. aspera*; C, D, *P. volúbilis*. A, B from *Aguilar 17367*; C from *Hammel 27784* (cult.), D from *Hammel 27118* (wild). Scale bars = 10 mm.

Note on the transfer of *Xolocotzia asperifolia* Miranda to *Petrea*. When Christenhusz & Byng (2018) transferred *Xolocotzia asperifolia* (an erect shrub or small tree of relatively xeric forests of Chiapas Mexico, Honduras, and Nicargua) to *Petrea* they unnecessarily created the new name *P. xolocotzia* under the assumption that "*Petrea asperifolia* Brongn." was blocking a direct transfer. However, the latter is nothing but a herbarium name, cited in synonymy by Moldenke (1938, p. 161) under *P. bracteata* Steud. (see Art. 36. 1, Turland et al. 2018); it was never published by Brongniart, let alone accepted or published as a distinct species by Moldenke nor anyone else since. As such it does not block the following transfer.

PETREA ASPERIFOLIA (Miranda) Hammel, **comb. nov**. Basionym: *Xolocotzia asperifolia* Miranda, Bol. Soc. Bot. México 29: 40. 1965. *Petrea xolocotzia* Christenh. & Byng.

The moderately supported finding of *Xolocotzia asperifolia* as nested in *Petrea* (Marx et al., 2010) was based on two collections of *P. volubilis* and one of *P. kohautiana* Presl, the later itself a synonym of *P. volubilis* according to Rueda (1994) — a fact that Marx et al. apparently overlooked. Marx et al. also erroneously reported their voucher (*Clark 6554*, US) as being from Ecuador, when in fact it was collected in Dominica. Nevertheless, their findings (*P. volubilis* would be polyphyletic by current taxonomy), if corroborated with further study, indicate that at least one other species, the Antillian *P. kohautiana*, should be resurected from synonymy. Only by the literature (and the few images we could find of Antillian *Petrea*), one obvious morphological character in support of that possibility are the terminal inflorescences of material formerly determined as that species (see, eg. Moldenke 1938; Nicholson 1991). In spite of including *P. kohautiana* in synonymy, Rueda (1994) only described axillary inflorescences for *P. volubilis*.

The Mesoamerican species of *Petrea* can be distinguished as follows:

1. Calyx tube densely pubescent to hirsute and with glandular trichomes, the calycine crest inconspicuous (1–1.5 mm in fruit) or lacking; leaves strongly scabrous.

    2. Erect shrub or small tree of relatively xeric sites; calyx not accrescent, deciduous in fruit, the lobes less than 10 mm long, calycine crest lacking; Mexico, Honduras, Nicaragua ..... **Petrea asperifolia**
    2. Liana (woody vine) or scandent shrub of relatively mesic sites; calyx accrescent and persistent in fruit, the lobes 8–21 mm long, calycine crest 1–1.5 mm; Mexico–Panama ..... **Petrea volubilis**

1. Calyx tube sparsely substrigulose to puberulent pilose, lacking glandular trichomes, the calycine crest conspicuous (2.5–4 mm in fruit); leaves smooth to subscabrous.

    3. Inflorescences axillary, the pedicels 5–11 mm; corolla tube 6–11 mm; Costa Rica and Panama ..... **Petrea aspera**
    3. Inflorescences terminal, the pedicels 10–31 mm; corolla tube 13–22 mm; eastern Panama ..... **Petrea blanchetiana**

or

1. Erect shrub or small tree of relatively xeric sites; calyx not accrescent, deciduous in fruit, the lobes less than 10 mm long, calycine crest lacking; Mexico, Honduras, Nicaragua .....**Petrea asperifolia**

1. Lianas (woody vines) or scandent shrubs of relatively mesic sites; calyx accrescent and persistent in fruit, the lobes 8–20(–26 in fruit) mm long, with a distinct calycine crest.

    2. Inflorescences terminal; corolla tube 13–22 mm; eastern Panama ..... **Petrea blanchetiana**
    2. Inflorescences axillary; corolla tube 6–11 mm.

        3. Calyx tube sparsely and minutely substrigulose, lacking glandular trichomes; Costa Rica and Panama ..... **Petrea aspera**
        3. Calyx tube densely hirsute and with scattered glandular trichomes; Mexico–Panama ..... **Petrea volubilis**

Figure 4. *Petrea aspera*. Mándala by R. Aguilar, from *Aguilar 17367* <https://www.flickr.com/photos/plantaspeninsulaosa/49956610856/in/photolist-2j7rHke-2j7ugN9-2j7w98m-2j7ugLW-2j7uFWQ/>.

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A NEW COMBINATION IN *MESPILODAPHNE* (LAURACEAE) FOR A COSTA RICAN *OCOTEA*

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ABSTRACT

In order to conform with recent phylogenetic classification within *Ocotea* as well as the taxonomy used in the Lauraceae treatment in Vol. VI of the *Manual de Plantas de Costa Rica*, the species treated therein as *Ocotea paradoxa* Mez is recognized here as **Mespilodaphne paradoxa** (Mez) Hammel, **comb. nov.**

Mespilodaphne paradoxa (Mez) Hammel **comb. nov.** Basionym: *Ocotea paradoxa* Mez, Bot. Jahrb. Syst. 30 (Beibl. 67): 16. 1901. *Ocotea klepperae* van der Werff; *M. klepperae* (van der Werff) Trofimov.

In light of their taxonomy that includes *Ocotea paradoxa* as a synonym of *Ocotea veraguensis* (Meisn.) Mez, while accomodating "*Ocotea dendrodaphne* group" species into their reinstatement of the mezian genus *Mespilodaphne,* Trofimov et al. (2019) had no reason to transfer said paradoxical *Ocotea* to *Mespilodaphne.* But I do, convinced, as I still am, by the taxonomy that considers *O. paradoxa* an older name for *O. klepperae* (see González & Hammel 2007).

Type material of *Ocotea paradoxa* (*Tonduz 7648*, BR!, CR!) is a good match to that of *O. klepperae* (*Hammel 22068*, CR!, MO!) and the type localities of said names are not far apart, both being from near the boundary between Puntarenas and San José provinces along the middle part of Costa Rica's Pacific coast, southeast of San Jose, in the coastal foothills of the northern part of the Cordillera de Talamanca just above Puerto Quepos. Each of these two species was diagnosed by its author as distinct from *O. veraguensis* using nearly the same words. Mez (1901) considered *O. paradoxa* close to *O. veraguensis* "insigniter toto habitu [frutex ramulis summo apiceo paullo ferrugineo-tomentellis, glabratis brunneis, teretibus, gemmis ferrugineo- vei flavido-tomentellis], inflorescentia pauciflora racemosaque, floris glandulis differt." And then somewhat later, perhaps without taking a second look at *O. paradoxa*, van der Werff (2001) distinguished *O klepperae* "from the other species in this subgenus in its dense indument on twigs, inflorescences, and flowers. *Ocotea klepperae* further differs from the common *O. veraguensis* (Meisn.) Mez and *O. dendrodaphne* Mez in having shorter inflorescences with fewer flowers."

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Serviss, B.E. and T.K. Serviss. 2020. Noteworthy records of *Pistacia chinensis* (Anacardiaceae) and *Ulmus parvifolia* (Ulmaceae) in Arkansas. Phytoneuron 2020-85: 1–4. Published 18 December 2020. ISSN 2153 733X

NOTEWORTHY RECORDS OF *PISTACIA CHINENSIS* (ANACARDIACEAE) AND *ULMUS PARVIFOLIA* (ULMACEAE) IN ARKANSAS

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ABSTRACT

Pistacia chinensis Bunge and *Ulmus parvifolia* Jacq. are reported here for their second occurrences in Arkansas outside of cultivation. Both species were discovered as escaped populations of multiple individuals in Clark and Garland counties, respectively. Both sets of escaped plants were seeded from cultivated plants of the two species that were located in the vicinity. The escaped/naturalized population of *U. parvifolia* represents the first documentation of extensive reproduction and localized establishment of this species in the state.

Escaped plants of *Pistacia chinensis* Bunge (Chinese pistachio) were discovered in 2020 at the edge of disturbed, roadside woods near the outer city limits of Arkadelphia (Fig. 1). These plants were juveniles (all less than 2 meters tall) established via seeds from cultivated plants of the species that were present in the vicinity. A total of 10 escaped plants were observed, with individuals occurring on either side of W. P. Malone Drive. Plants were clustered in two locations, under trees, where (anecdotally) it appeared the seeds were deposited by roosting birds that had ingested fruits produced by the cultivated *P. chinensis* plants. McWilliams (1991) noted bird-mediated dispersal of *P. chinensis* in Texas, with similar observations to the above for occurrence and establishment of juvenile plants.

A second location from Clark County, also within the city of Arkadelphia, had 14 escaped plants that also appeared to be established via seeds deposited by birds (Fig. 2). These plants occurred in an unkempt, street side tree and shrub bed; similar establishment by *P. chinensis* also was documented by Krings (2011) in North Carolina. The closest reproductively mature *P. chinensis* plants are cultivated individuals located more than two blocks away — these are the presumed source of the escaped plants. A number of other woody, bird-dispersed species, all as juveniles, also were present at the site, including *Ampelopsis cordata*, *Parthenocissus quinquefolia*, *Podocarpus macrophyllus*, *Prunus serotina*, *Pyrus calleryana*, and *Sassafras albidum*.

Voucher specimens. **Arkansas.** Clark Co.: Arkadelphia, off W.P. Malone Dr., ca. ¼–½ miles N of intersection of Pine St. and W.P. Malone Dr., 10 escaped, juvenile plants distributed on both sides of the road, at edge and slightly within disturbed, roadside woods, seeded in from cultivated plants in the vicinity, 10 Nov 2020, *Serviss 8745* (HEND); Arkadelphia, at NW corner of intersection of 12th St. and Henderson St., highly disturbed area of tree and shrub bed, 14 escaped plants, all juveniles, presumably seeded in from cultivated plants a few blocks away, 12 Jun 2020, *Serviss 8728* (HEND).

Pistacia chinensis first was documented from the Arkansas flora in 2011 from Pulaski County (Peck & Serviss 2011). The discovery of the 2020 Clark County plants provides two additional escaped occurrences of the species in the state. *Pistacia chinensis* is a medium-sized, deciduous tree to 20 meters that is native to China (Krüssmann 1977; Min & Barfod 2008). In addition to Arkansas, it has been documented from the floras of a number of other southern states (Krings 2011; Kartesz 2015; Invaders of Texas/Texas Invasives 2020; USDA, NRCS 2020).

Figure 1. (A–B) Two escaped plants of *Pistacia chinensis* in Clark Co., Arkansas. A total of 10 escaped plants occurred clustered in two locations, one on either side of a road. Several cultivated plants of *P. chinensis* were present in relative close proximity to the escaped individuals; however, they were separated from them by several meters. Bird-mediated dispersal and deposition of seeds from the cultivated *P. chinensis* plants is the presumed means of establishment.

Figure 2. Escaped, juvenile plants of *Pistacia chinensis* in Clark Co., Arkansas. These plants are from a different location than those shown in Figure 1. Fourteen (14) individuals were present at the site, which consisted of a roadside, ornamental bed of trees and shrubs; two of the *P. chinensis* plants can be seen in the photograph (lower-left and upper-right). Similar to the other Clark County site, establishment of the escaped plants is presumed to be via bird-mediated seed dispersal from cultivated *P. chinensis* plants.

Also in 2020, a large, escaped/naturalized population of *Ulmus parvifolia* Jacq. (Chinese elm, lacebark elm) was discovered in Garland County, within the city of Hot Springs (Fig. 3). The population occurred along a disturbed, urban greenbelt, and consisted of numerous naturalized plants, ranging in size from less than a meter to several meters in height. The source of the population appeared to be a few cultivated, reproductively mature plants of the species in proximity to the greenbelt, with establishment via seed production from the cultivated plants, which had nearly mature fruits at the time of discovery.

Voucher specimen. **Arkansas.** Garland Co.: Hot Springs, off Central Ave., immediately E/SE of intersection of Mehta Ct. and Central Ave., large, escaped/naturalized population of mostly juvenile plants scattered along a disturbed, urban greenbelt, seeded in from cultivated plants in the vicinity, 21 Aug 2020, *Serviss 8731* (HEND).

Ulmus parvifolia first was documented from the Arkansas flora in 2016 from Garland County (Serviss et al. 2016); however, the 2016 location was not in Hot Springs and did not represent a naturalized population. The 2020 Garland County record provides the first direct evidence of extensive reproduction and naturalization of *U. parvifolia* in the Arkansas flora, on a localized basis, and represents its second documented occurrence in the state outside of cultivation.

Figure 3. Escaped/naturalized plants of *Ulmus parvifolia* in Garland Co., Arkansas. Five (5) plants can be seen in the photograph, all juveniles (designated be yellow arrows). The entire population consists of numerous plants scattered throughout a highly disturbed, urban greenbelt.

Ulmus parvifolia is a medium to large, deciduous tree to 25 meters tall that is native to China, Japan, and Korea (Krüssmann 1978; Fu et al. 2003). In addition to Arkansas, it has been

documented from the floras of a number of other states (Sherman-Broyles 1997; Thomas & Allen 1998; Wunderlin & Hansen 2011; Kartesz 2015; USDA, NRCS 2020).

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FIRST REPORT OF *PERSICARIA POSUMBU* (POLYGONACEAE) FOR NORTH AMERICA

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ABSTRACT

Persicaria posumbu, a smartweed from eastern Asia, is naturalized in populations on the Delaware River floodplain in New York and New Jersey — the first report of its spontaneous occurrence in North America. Documentation is provided by herbarium specimens preserved at the New York Botanical Garden and photographs uploaded to iNaturalist.

Plants of *Persicaria posumbu* (Buch.-Ham. ex D. Don) H. Gross have been found on floodplains of the Delaware River in Sullivan Co., New York, and Warren Co., New Jersey. This is the first report of this species growing spontaneously in North America (Hinds & Freeman 2005; USDA, NRCS 2020).

By the most improbable coincidence, on the same day and unbeknownst to the other, the authors observed populations of the *Persicaria* 85 miles apart: Atha in New York and Rall in New Jersey. Noting each other's observations uploaded to iNaturalist, a conversation ensued and two days later the first author returned to the New York population to make additional observations and collect herbarium specimens.

The New York plants did not key out in the recent FNA treatment (Hinds & Freeman 2005), nor were identifiable in the Flora of Pennsylvania (Rhoads & Block 2007), Flora Novae Angliae (Haines 2011), Flora of Virginia (Weakley et al. 2012), Flora of Vermont (Gilman 2015), Flora of Cortland and Onondaga Counties, New York (Hough 2019), and others. On suspicion that the plants might be another undocumented taxon for North America (Atha et al 2010; Atha & Carr 2010), keying the plants in the Flora of China (Li et al 2003) and the Flora of Taiwan (Huang et al. 1996) led to *Persicaria posumbu* (compare Figs. 1 and 2 with Figs. 3 and 4).

The New York population consists of hundreds or perhaps thousands of plants (Fig. 2) occupying an area of about 100 square meters in the alluvial floodplain of the Delaware River. The overstory consists of *Fraxinus americana*, *Tilia americana* and *Acer rubrum* with *Quercus rubra* and *Tsuga canadensis* in slightly upland areas. The herbaceous layer is dominated by *Persicaria posumbu* with scattered occurrences of *Persicaria virginiana*, *Ageratina altissima*, *Parthenocissus quinquefolia* and a dense covering of *Glechoma hederacea*. Somewhat smaller populations of *Persicaria longiseta* and *Persicaria nepalensis* occur nearby, the former growing with the *P. posumbu* (iNaturalist observations 58847228, 65565292, 65565293, 65565294, 65598441).

Vouchers. **New York.** Sullivan Co.: Village of Long Eddy, between the Delaware River and NY Hwy 97 and between Church Street and Basket Brook Road. 41.847817, -75.131298 (WGS84, ±5m), 9 Sep 2020, *Atha 16168* (NY), *16169* (NY), *16170* (NY), *16171* (NY), *16172* (NY), *16173* (BH, NY).

Two populations of *Persicaria posumbu* were found in New Jersey. They consist of a few dozen to several dozen plants in two separate sites about one kilometer apart, one of about 20 square meters and one of about 3 square meters, both in the alluvial floodplain of the Delaware River, separated from the river by a freight railway. The larger population is at the base of a north-facing cliff with an overstory of *Robinia pseudoacacia*, *Acer saccharum*, and *Acer saccharinum*, with an understory of *Hamamelis virginiana* and *Lindera benzoin*. Undergrowth is dominated by *Persicaria posumbu*, *Glechoma hederacea*, and *Microstegium vimineum*, with scattered *Anthriscus sylvestris*, *Stellaria aquatica*, and *Pilea pumila*. (iNaturalist observations 59073673, 59073639, 59073638).

The smaller New Jersey population is at the base of a west-facing cliff with an overstory of *Juglans nigra*, *Carya cordifolia*, and *Quercus montana* with scattered *Sassafras albidum* and *Hamamelis virginiana*. Undergrowth is dominated by *Lonicera japonica*, *Microstegium vimineum*, and *Persicaria posumbu*, with scattered *Verbesina alternifolia*, and *Anthriscus sylvestris*. *Persicaria longiseta* and *Persicaria virginiana* also are present, within several meters (Fig. 1). (iNaturalist observation 59039385).

Morphology

Persicaria posumbu is most easily confused with *Persicaria longiseta*. A collection of the latter (*Wheeler 5591*(x2), NY) has been misidentified as *P. posumbu*. The two species can be distinguished by the following key.

1. Leaves rhombic, bases cuneate, apices acute, adaxial and abaxial surfaces glabrous, purple blotch absent or faint, marginal bristles 0.1–0.3 mm long; inflorescences dense, fascicles congested (interrupted basally); pedicels included; proximal bracteole bristles surpassing the adjacent flowers; tepals dark pink, closed at anthesis; achenes < 2 mm long ..... **Persicaria longiseta**

1. Leaves elliptic, bases rounded and abruptly cuneate to the petiole, apices caudate, adaxial and abaxial surfaces strigose, purple lunate blotch conspicuous and present at maturity, marginal bristles 0.5 mm long; inflorescences lax, fascicles remote; pedicels exserted; proximal bracetole bristles scarcely reaching the base of the tapals; tepals pale pink to white, open at anthesis; achenes > 2 mm long ..... **Persicaria posumbu**

Persicaria posumbu can be distinguished from all other North American *Persicaria* by the following suite of traits: Low annual; eglandular; stems branched near the base, glabrous; ocreae strigose with terminal bristles 3–7 mm long; leaf blades elliptic, bases rounded and abruptly cuneate, the apices distinctly caudate, margins ciliate with bristles ca. 0.5 mm long, abaxial and adaxial surfaces strigose, bright green, adaxial surface with a prominent lunate purple blotch at maturity; inflorescences mostly terminal, lax, up to 15 cm long (including the peduncle), fascicles usually 3-flowered; bracteoles (ocreoleae) with terminal bristles ca 1 mm long, about as long as the exserted pedicels; tepals light pink to white, many opening to expose the barely exserted, white stamens; achenes all trigonous, 2.3–2.5 mm long and 1.5 mm wide, dark brown, lustrous.

It is not known when or how *Persicaria posumbu* arrived in North America. But it is interesting to note that *Persicaria nepalensis* (Meisn.) H. Gross was first found in the Catskill Mountains of New York (not far from Long Eddy) and in neighboring Connecticut before expanding more widely. The species was present at the New York site of *P. posumbu.* The authors have not searched the intervening nearly one hundred miles of Delaware River floodplain for more plants, but it seems unlikely that these three populations are the only occurrences of the species in the region.

Figure 1. *Persicaria posumbu*. Warren Co., New Jersey, 7 Sep 2020. Photo 94301836, (c) Sara Rall, some rights reserved (CC BY-NC) <https://www.inaturalist.org/observations/59039385>.

Figure 2. *Persicaria posumbu*. Sullivan Co., New York, 7 Sep 2020. Photo 105610685, Daniel Atha, no rights reserved. <https://www.inaturalist.org/observations/65598441>

Figure 3. *Persicaria posumbu*. South Korea, Jeollabuk-do, KR. 1 Sep 2020. Photo 103585298, (c) Yanghoon Cho, all rights reserved. <https://www.inaturalist.org/observations/64430382>

Figure 4. *Persicaria posumbu*. Taiwan, New Taipei, 30 Oct 2019. Photo 55295066, (c) (Bunny-TailGra22), some rights reserved (CC BY-NC-SA). <https://www.inaturalist.org/observations/35080170>

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FIRST REPORT OF *CROTON GLANDULOSUS* (EUPHORBIACEAE) FOR NEW YORK

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ABSTRACT

Croton glandulosus is naturalized in New York. Populations are documented from Queens and New York (Manhattan) counties, the first occurrences of the species and the first species of *Croton* to become established in the state. Documentation is provided by herbarium specimens at NY and photographs uploaded to iNaturalist.

Plants of *Croton glandulosus* L. were found by chance in late 2019 and 2020 during routine observation of the flora and fauna of New York City. Observations were uploaded to iNaturalist and identification of these observations was confirmed by the Euphorbiaceae specialist Nathan Taylor. This is the first report of this species growing spontaneously in New York State (van Ee & Berry 2016; Werier 2017; USDA, NRCS 2020) and the first *Croton* to become naturalized in the state (see Werier 2017 reference to *Croton capitatus* on Staten Island).

The genus *Croton* is one of the largest genera of the Euphorbiaceae with 1250 species worldwide and 31 in North America north of Mexico (van Ee & Berry 2016). Five varieties of *Croton glandulosus* are known from North America north of Mexico. The New York plants have leaf blades 3–7 cm long, sparsely pubescent with pointed marginal teeth (Fig. 1) and key to *Croton glandulosus* var. *septentrionalis* Müller Arg.

Voucher. **New York.** Queens Co.: New York City, Edgemere, S sidewalk of Rockaway Beach Blvd near the intersection of Rockaway Beach Blvd and Beach 41st Street, 29 Sep 2019, *Wang 98* (NY).

The Manhattan (New York Co.) population (Fig. 2) consisted of about a dozen plants growing at the edge of a basketball court and a concrete retaining wall (iNaturalist observations 59354391, 59354419, 59354600, 59501674, 59501722, 59501761, 59501818, 59501849, 59501906, 59501974, 59502036, 59502101, 59502247, 59502278, 59539968, 59784426, 59790865).

The Queens population (Fig. 3) consisted of a several plants growing in a sidewalk crack between the road and sidewalk (iNaturalist observation 33627601). Associated species include *Setaria pumila, Mirabilis nyctaginea, Ambrosia artemisiifolia, Medicago sativa*, and *Artemisia vulgaris*.

The two New York City populations are separated by 25 km of the densest urbanized area in North America and it seems improbable that these are the only two populations that occur (despite the intensive biodiversity monitoring by the naturalist community in New York City and shared observations and identifications through iNaturalist). We therefore suggest that the plants meet the

criteria for "established" rather than merely "adventive" as described by Nesom (2000). There are several scattered populations documented in adjacent New Jersey. The nearest, near Keansburg, Monmouth County (iNaturalist observations 17255555 and 7636202) is a mere 33 kilometers across Sandy Hook Bay from the Queens population.

Hurricane Sandy, which made landfall near Atlantic City, New Jersey, in 2012 and moved north across Sandy Hook and Lower New York Bays into New York City, could have carried seeds into New York. Destruction from the hurricane and subsequent demolition created additional areas suitable for growth of the species such as sand dunes, old fields, roadsides, and waste places. Such habitat is extensive on the Rockaway Peninsula of Queens where additional populations are likely to be found.

Figure 1. *Croton glandulosus* var. *septentrionalis*. New York Co., New York, 16 Sep 2020. Photo 59790865, Daniel Atha. < https://www.inaturalist.org/observations/59790865>

Figure 2. *Croton glandulosus* var. *septentrionalis*. New York Co., New York, 16 Sep 2020. Photo 95559884, Daniel Atha. <https://www.inaturalist.org/observations/59790865>

Figure 3. *Croton glandulosus* var. *septentrionalis*. Queens Co., New York, 29 Sep 2019. Photo 52831982, Zihao Wang. <https://www.inaturalist.org/observations/33627601>.

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OXALIS HISPIDULA (OXALIDACEAE) NATURALIZED IN LOUISIANA

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ABSTRACT

Oxalis hispidula is reported as naturalized in the Louisiana flora and west of the Mississippi River for the first time. It occurs on roadsides, sidewalk margins, and lawns in Caddo, Bossier, Natchitoches, Lafayette, and Ouachita parishes. It appears to spread easily and grows in dense concentrations where it has become established.

A paper published in Phytoneuron nearly a decade ago (Horne et al. 2013) inspired me to seek new records for naturalized and persistent *Oxalis* species in my region. In the summer of 2020 I was given a sample from a native plant enthusiast which appeared to be *Oxalis hispidula* Zucc., but the sample was only vegetative. In the fall of 2020, I discovered multiple populations of the same entity, this time with diagnostic material, in Caddo, Natchitoches, Lafayette, and Bossier parishes and I received a trustworthy report of its occurrence in Ouachita Parish. Major floristic resources do not list Louisiana within the range of this plant, and none record it west of the Mississippi River (Kartesz 2014; USDA 2014; Nesom 2016; SERNEC 2020; Weakley 2020).

A risk assessment of *Oxalis hispidula* developed by the USDA suggested Louisiana was climatically favorable to the species and considered it a "minor invader" (USDA 2016). At this time, the plant seems to pose no threat to natural communities or imperiled species.

In Louisiana, plants occur in large colonies (up to 0.5 hectares loosely), the height often reduced by mowing, in wet ditches and roadbanks, along park trails, and in suburban lawns. Multiple small populations are known in the five parishes, and the plant is likely widespread and unrecognized in other urban and suburban areas. It frequently occurs with lawn grasses and other invasive and weedy species such as *Wisteria sinensis, Cynodon dactylon, Paspalum urvillei,* and *Axonopus fissifolius.* All areas receive frequent mowing or foot traffic.

Allen Weakley (pers. comm.) observes that this species is widespread and forms large colonies in neighborhoods of Monroe, Ouachita Par., Louisiana. Photos from iNaturalist suggest that it is likely present in Texas, but the observations do not give enough evidence for me to declare its naturalization there or in Louisiana parishes other than the ones noted above.

The species is perennial by nature, and detritus at observed stations suggested that plants have been established in Louisiana for multiple seasons. They are acaulescent with villous flowering scapes and petioles, abaxially strigose leaflets with their conjoined bases densely pubescent and margins consistently ciliate, purple corollas accented by deep purple veins, acute sepal apices with elongated orange tubercles, and few-nerved bulb scales.

Vouchers. Louisiana. Caddo Par.: Shreveport, along South Lakeshore Drive, large patch in an apparently non-domestic site, with other non-natives and weeds, 32.5015, -93.8772, 11 Nov 2020, *Kelley* 621 (LSUS, LSU). Bossier Par.: Bossier city, lawn N of Brookshires Grocery W of US-71, with Bermuda grass, covering ~1/20 ha. in near carpet density, 11 Nov 2020, *Kelley* 622 (LSU). Natchitoches Par.: Natchitoches, Henry Ave and East 3rd, lawns and along roadsides in large clumps, 12 Nov 2020, *Mcelwee* s.n. (LSU). Lafayette Par.: Lafayette, lawn of ULL Online Programs facing Johnston St. and between Ira Nelson Horticulture Center and Coliseum Rd, plants in patches up to thousands with other non-natives and weeds near building, 22 Nov 2020, *Vincent* 97 (LSU).

Figure 1. *Oxalis hispidula* sepals with tubercles (top left), leaflets with ciliate margins and strigose

laminae (top right), and general habit in a lawn of about 0.1 ha (bottom).

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MORPHOLOGY AND DISTRIBUTION OF *HETEROTHECA CAMPORUM* VAR. *GLANDULISSIMA* AND ITS OCCURRENCE ON SHALE SUBSTRATES IN NORTHEASTERN TENNESSEE

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ABSTRACT

The geographical range of *Heterotheca camporum* var. *glandulissima* is expanded to include four counties in northeastern Tennessee. Most of the newly reported occurrences are found in the Booher Knobs region, an area of shale knobs overlain with Montevallo soils. Large populations occur at several localities, often associated with quarries and roadsides but occasionally in more natural sites. In this region, there appears to be high fidelity to the shale substrate. The morphology of the northeastern Tennessee plants was similar to prior descriptions of *H. camporum* var. *glandulissima* except on some plants peduncle and phyllary glands were sparse or absent. There is evidence of population differentiation for the density of phyllary glands. The species appears to have undergone relatively recent proliferation in the shale belt but the time of initial colonization of the region and the shale knobs remains questionable.

The genus *Heterotheca* (Asteraceae) is restricted to North America and Mexico with a center of diversity in the Great Plains and southwestern U.S. (Harms 1963; Semple 1996, 2006; Nesom 2020). *Heterotheca camporum* (Greene) Shinners is the easternmost representative of the *H. villosa* species group of sect. *Phyllotheca* (Harms 1963; Semple 2006; Nesom 2020). Although H. *camporum* is uniformly tetraploid (2n = 36) throughout its range, observations of geographically based morphological variation have been noted for plant height, leaf width, leaf margin teeth, and leaf and phyllary pubescence and glandularity (Harms 1963; Semple 1983). There are indications that plants from northern parts of the geographical range have narrower leaves and are more densely glandular on upper stem leaves and phyllaries. However, Harms (1963) concluded that an absence of correlations among these characters and range-wide variability in most characters argue against recognition of subspecific taxa. Further, an environmental influence on the variable characters was detected in two common garden experiments, one based on seedlings and the other on transplants (Harms 1963; Nesom 2020) but in an experimental transplant of rootstocks, the dense glandularity remained fixed (Semple 1983).

While acknowledging range-wide variation in most morphological characters, Semple (1983) nevertheless, showed that plants from the eastern part of the geographical range (Alabama, Kentucky, North Carolina, Tennessee) tend to be taller in stature with more glandular but less pubescent upper stems, peduncles, and phyllaries. On the basis of this geographically based morphological differentiation, Semple recognized *Heterotheca camporum* var. *glandulissima* Semple. Moreover, an examination of herbarium specimens showed that var. *glandulissima* had recently colonized the eastern portion of its current range, having been absent prior to 1925 (Semple 1983). From 1925 to 1949 the species became widespread in central Tennessee and reached one county each in northern Alabama and central Kentucky. Further range expansion, south to Mississippi, north to Virginia, and east to eastern North Carolina occurred from 1950–1983 (Semple 1983). The range of var. *glandulissima* was subsequently updated to include western Arkansas and western Missouri (Semple 1996).

Under Semple's varietal delineation, *Heterotheca camporum* var. *camporum* is "endemic to limestone bluffs, cedar glades, and sandy prairie in the Prairie Peninsula region of the midwestern U.S." extending south to eastern Missouri and northern Arkansas at elevations of 100–300 meters. East of the Mississippi River, the distribution of var. *glandulissima* is allopatric with var. *camporum*, with locations in central Tennessee east to the Ridge and Valley physiographic province of Tennessee and Virginia, where it is found on "limestone bluffs and glades, roadsides, fields, and disturbed areas" and up to more upland elevations (30–760 m) (Cronquist 1980; Semple 1983, 1996). Nesom (2020) updated the distribution of var. *glandulissima* by adding sites throughout the Southeast as well as expanding the region of parapatry to var. *camporum* in northern Arkansas and southern Missouri.

The goal of this study was to further update the geographic range of *Heterotheca camporum* var. *glandulissima* with an emphasis on fine-scale analysis of occurrences in northeastern Tennessee and to conduct a comparison of diagnostic morphology of specimens from the new locations to literature descriptions. The relationship of var. *glandulissima* to shale and shale-derived soils was examined for southeastern specimens. In addition, a locality for *H. subaxillaris* (Britton & Rusby) that was located in 2015 was examined to determine whether the species has established in the region. These goals were accomplished by field work in northeastern Tennessee and an examination of herbarium specimens using the SERNEC online database (SERNEC 2020).

METHODS

Study site

Localities were most intensively searched from 2017–2020 in the three-county area of Carter, Sullivan, and Washington cos., Tennessee, with an emphasis on the region referred to (on some topographic maps) as the Booher Knobs (Figs. 1, 2). These knobs trend southwest to northeast with a long axis represented in the southwest as two fingers in Johnson City (Washington Co.) extending northeast to Bluff City (Sullivan Co.), and ranging on the short axis from Watauga (Carter Co.) on the southeast, north to Piney Flats (Sullivan Co.). The knobs are easily recognized as highly dissected, steep, low hills (elevation 460–580 m) (Fig. 2B). The area is underlain by rocks of the Sevier Shale (Middle Ordovician), comprised in northeastern Tennessee a series of light blue calcareous shales that weather to yellowish-brown channery loam soils (Keith 1895; Prouty 1946; Hardman et al. 1966; Nandi et al. 2009) (Figs. 1C, 2, 3). Montevallo soils dominate the uplands of the Booher Knobs. On moderate to steep slopes, these soils are acid, well-drained, low in organic matter and therefore subject to drought (Davis 1994).

Exploration of the knobs of northeastern Tennessee was part of a larger floristic study of the knobs. A characteristic flora, composed of species not common elsewhere in the region, is associated with the Montevallo soil of the knobs. The shale has been mined at several quarries in the region, some currently in operation and many that were small, abandoned, and not reclaimed, leaving a substrate devoid of topsoil but a surface dominated by exposed loose shale with fragments approximately 1–8 cm^2 in size (Figs. 1, 4). The study of *Heterotheca camporum* was initiated particularly because it appeared to have some fidelity to this geographically distinct area, i.e., the species was widespread and abundant there but relatively scarce elsewhere in the region.

Geographic distribution and habitat

The SERNEC (2020) database was searched for specimens in states of the southeastern USA, i.e., the hypothesized recently colonized region, to update the geographic distribution and to use specimen label data to assess associations with substrate and soil. Particular emphasis was placed on whether there were prior reports of the species in knob-like topography or on shale-derived soil. For the northeastern Tennessee region, field collections from the knobs region were made during the 2017–2020 growing seasons.

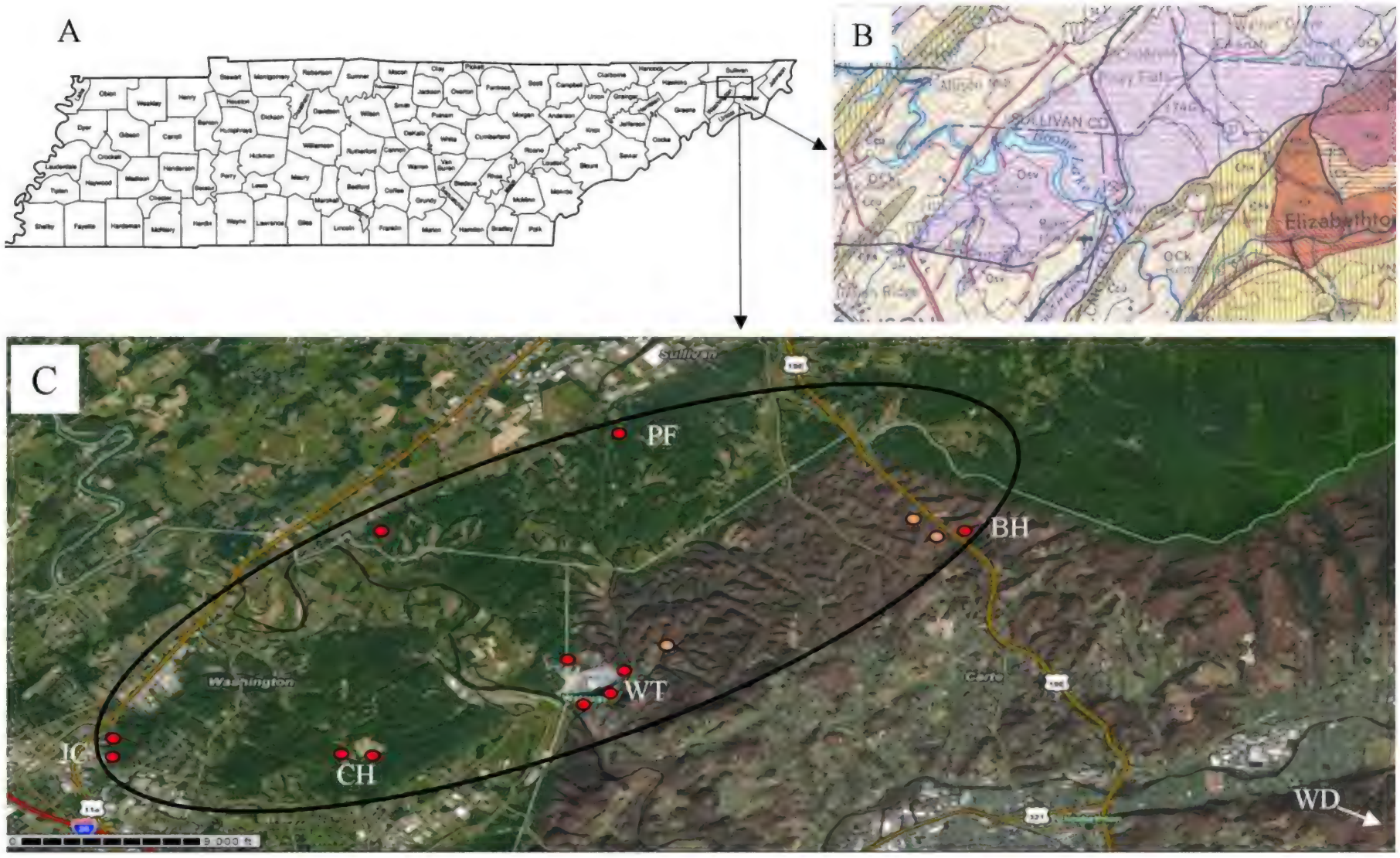

Figure 1. Location of the Booher Knobs in northeastern Tennessee. A. Map of Tennessee with ellipse highlighting study location encompassing parts of Carter, Sullivan, and Washington County. B. Portion of geological map showing the Sevier Shale (pink) northwest of Elizabethton and northeastern of Johnson City (map from Hardman et al. 1966). C. Air photo of the study location showing collection sites for *Heterotheca camporum* var. *glandulissima* specimens used in the morphological analysis (red dots) and other sites with abundant populations (pink dots). The large quarry visible due south of the three-county boundary is located in the town of Watauga. Population acronyms; BH = Bunker Hill, CH = Cash Hollow, JC = Johnson City, PF = Piney Flats, WD = Watauga Dam, WT = Watauga Town

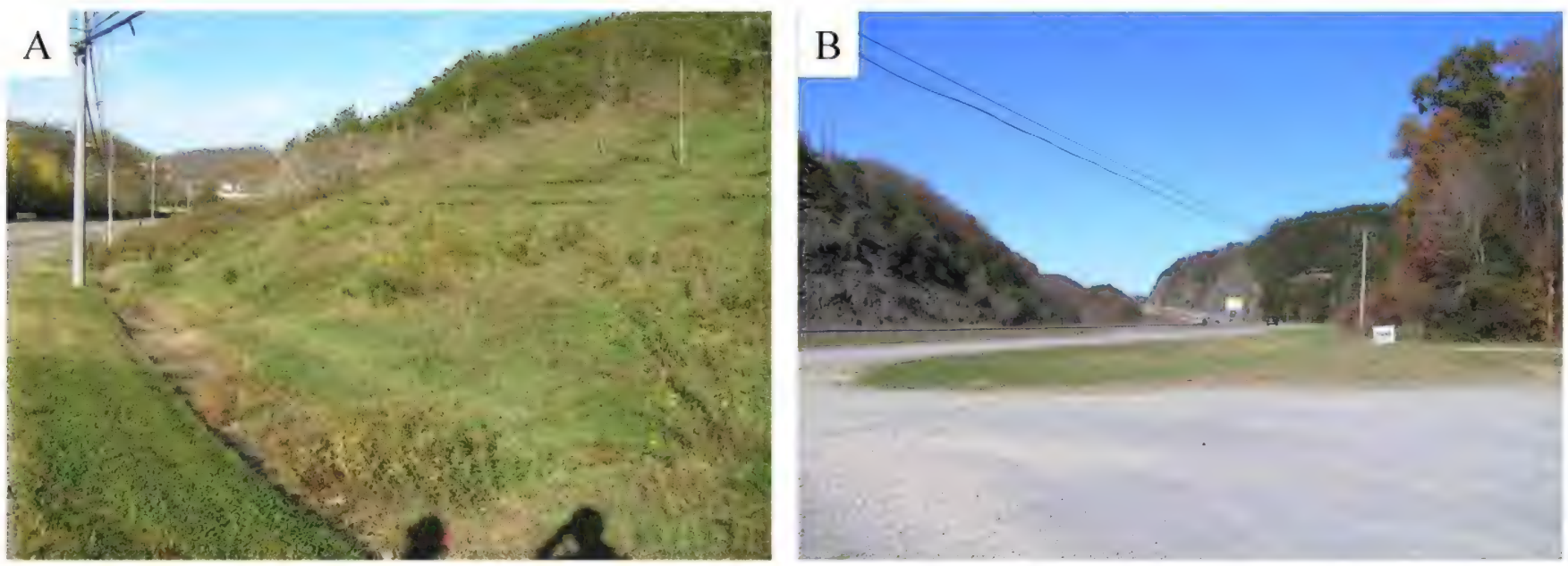

Figure 2. The Booher Knobs region of northeastern Tennessee. A. Disturbed area at the southern finger of the region in Johnson City with scattered plants of *Heterotheca camporum* var. *glandulissima*. B. Road cuts through the shale knobs looking north along Rt. 19E towards Bunker Hill. Plants are abundant in some areas of these road cuts and roadsides.

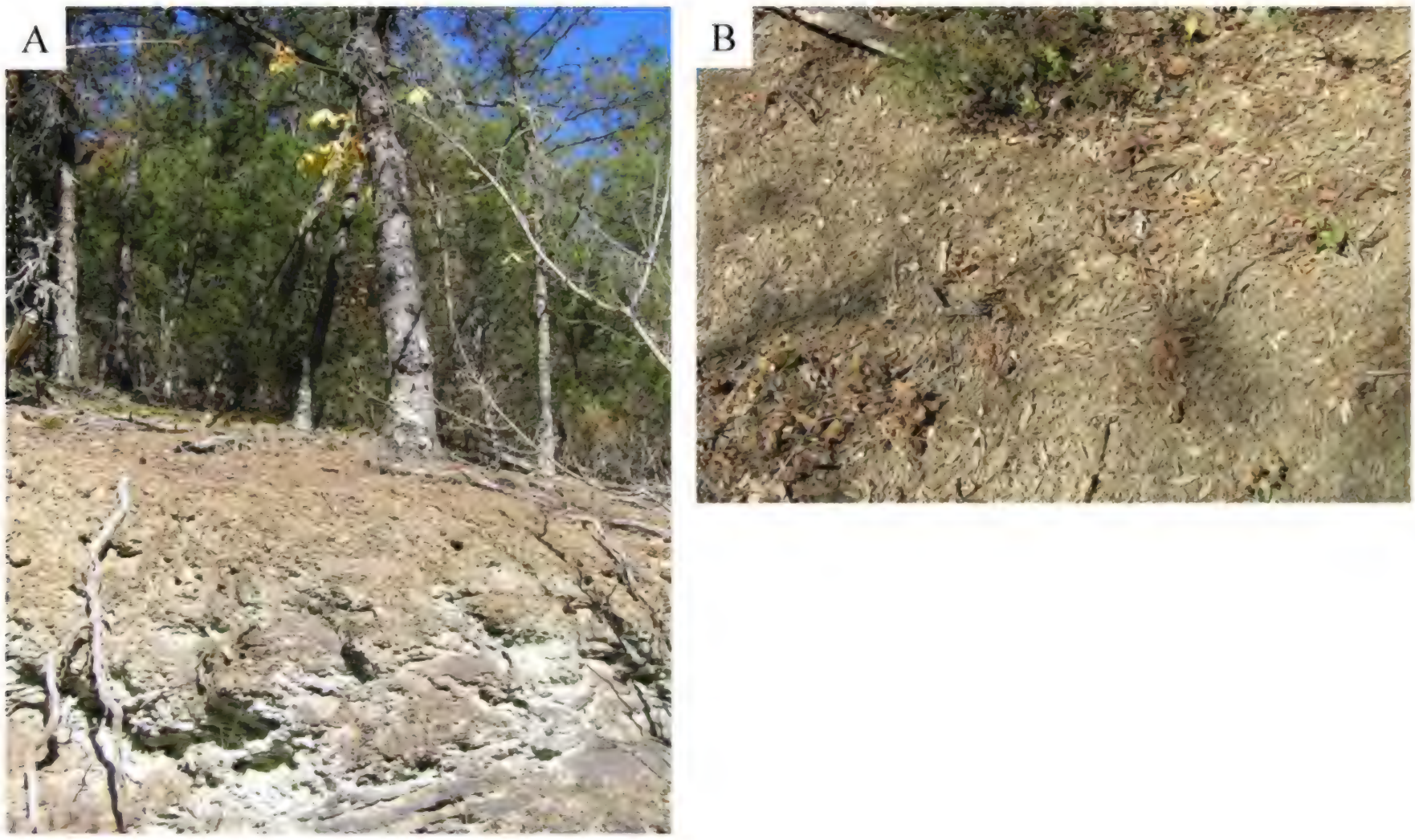

Figure 3. A. Natural outcropping of the Sevier Shale on a south-facing slope with *Pinus virginiana* in the background. B. Yellowish-brown channery loam of the Montevallo soil.

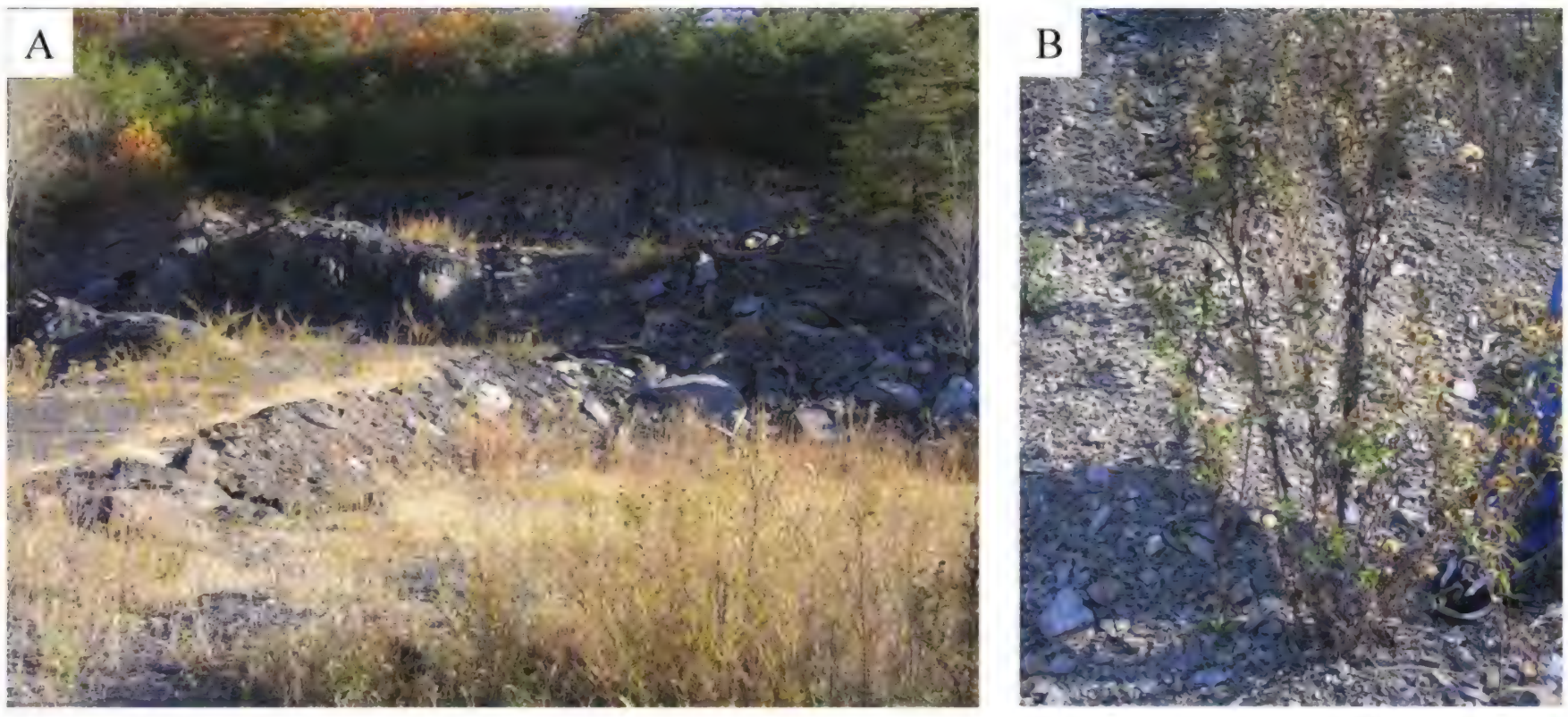

Figure 4. A. Abandoned quarry with *Heterotheca camporum* var. *glandulissima* in the foreground and *Pinus virginiana* in the background. B. Tall plant (~110 cm) of *H. camporum* var. *glandulissima* growing directly in the shale debris of former quarry.

Morphology

A morphological analysis was carried out to quantify the density of glands and hairs on diagnostic tissues, determine if plants from the shale region were similar to those in the remainder of the range of *Heterotheca camporum* var. *glandulissima*, and determine whether there were differences among populations within the shale region. The sample consisted of 27 plants from six populations, five in the Booher Knobs and one at Watauga Dam, with 3–6 plants per population. All plants were collected within a 5-day span to minimize potential seasonal influences on morphology. Nine characters were measured, all except leaf length and width chosen because they were diagnostic for *H. camporum* var. *glandulissima* (Table 1). A correlation analysis was carried out with significance based on the Pearson correlation coefficient, and an analysis of variance was conducted for each character to determine if populations differed. Analyses were carried out using SAS v. 9.4 (SAS Institute Inc. 2016).

RESULTS

Heterotheca camporum var. *glandulissima* was collected from seven northeastern Tennessee localities within the tri-county Booher Knobs area (Fig. 5), one locality at Watauga Dam (Carter Co.), and one locality at the Holston Army Ammunition Plant (Greene Co.). All of the Booher Knobs localities were from shale substrates including four in proximity to quarries and the remainder from roadsides and adjoining open areas. Distinctions between "populations" at some locations was relatively subjective because plants were exceedingly abundant and occurred in more or less continuous distributions along roadsides or in quarries and adjoining areas. The species was often the dominant one where it occurred or was intermixed with exotics such as *Lespedeza sericea* and natives such as *Solidago speciosa*, *Symphyotrichum pilosum* var. *pilosum* and *Vernonia gigantea*.

In the ETSU herbarium, older specimens of *Heterotheca camporum* var. *glandulissima* (collection dates ranged from 1976–1995) from beyond the knobs region include one sheet from the Watauga Dam locality, one from Warrior's Path State Park (Sullivan Co., probably a dolomite substrate), and two from indefinite locations in Johnson City (Washington Co.). There were also five sheets from the shale knobs collected in 2018.

A persistent (> 5 years) population of *Heterotheca subaxillaris* was found in proximity to the railroad yard at Erwin (Unicoi Co.). The species is common along the margins of the railroad tracks, in the yard area, and along the periphery of the adjacent roadside for a distance of about 0.5 km. Traveling east, this railroad yard is located in the final town prior to entering the Nolichucky River gorge, a major artery for transport of coal from Kentucky and West Virginia to the Piedmont of North Carolina. Similarly, in Tennessee, *H. subaxillaris* has been reported in proximity to railroads in Davidson, Knox, Marshall, and Sumner cos., Tenn (SERNEC 2020).

The morphology of *Heterotheca camporum* var. *glandulissima* from northeastern Tennessee is largely consistent with the original literature description in having sparse phyllary pubescence but abundant glands and peduncles and upper stems that were more glandular and less pubescent (Table 1, Fig. 6). Plant height was exceptionally variable — plants less than 20 cm on debris-strewn rocky quarry sites may flower but in deeper substrates some plants attained the reported tall stature (> 120 cm). Leaf length and width were the only variables with a significant correlation ($r = 0.78$, $P < 0.0001$). There were significant differences among populations only for the density of phyllary glands (fig. 6). An a posteriori test showed plants from Cash Hollow (CH) tended toward a higher density of glands compared to Piney Flats (PF), Bunker Hill (BH), and Watauga Dam (WD) but not significantly more than Johnson City (JC) or Watauga Town (WT) (ANOVA: $F_{5,21} = 4.78$; $P = 0.005$; means: CH = 14.6,WT = 11.0, JC = 10.8, WD = 5.3, PF = 5.0, BH = 4.0).

Table 1. Characters measured and their means and ranges for the morphological analysis of *Heterotheca camporum* var. *glandulissima* from northeastern Tennessee. Measurements from Semple (1983) are shown for comparison. Sample size = 22–27 per character, densities expressed as number per 1.0 x 0.2 mm rectangle, s.d. = standard deviation of the mean, n.d. = not done

Character	Description	Mean (s.d.)	Range	Semple (1983) Mean (Range)
Height (cm)	stem base to top of highest head	67.3 (13.8)	46–103	95.7 (35–140)
Upper leaf length (mm)	leaf 10 cm from bottom of lowest inflorescence branch	47.5 (11.6)	26–74	35.3 (15–70)
Upper leaf width (mm)	leaf 10 cm from bottom of lowest inflorescence branch	10.5 (3.4)	4–16	7.2 (2–16)
Upper stem glands	number of glands per 1.0 x 0.2 mm rectangle; 3 cm from lowest inflorescence branch	13.5 (7.1)	3–32	few/many
Upper stem hairs	number of hairs per 1.0 x 0.2 mm rectangle; 3 cm from lowest inflorescence branch	1.4 (1.1)	0–4	n.d.
Peduncle glands	number of glands per 1.0 x 0.2 mm rectangle; 1 cm below uppermost head	13.3 (9.3)	2–42	many
Peduncle hairs	number of hairs per 1.0 x 0.2 mm rectangle; 1.0 cm below uppermost head	2.5 (2.3)	0–8	n.d.
Phyllary glands	number of glands per 1.0 x 0.2 mm rectangle; from phyllary upward curve of the second phyllary series from outside	8.9 (5.5)	0–22	many
Phyllary hairs	number of glands per 1.0 x 0.2 mm rectangle; from phyllary upward curve of the second phyllary series from outside	0.6 (0.9)	0–3	sparse

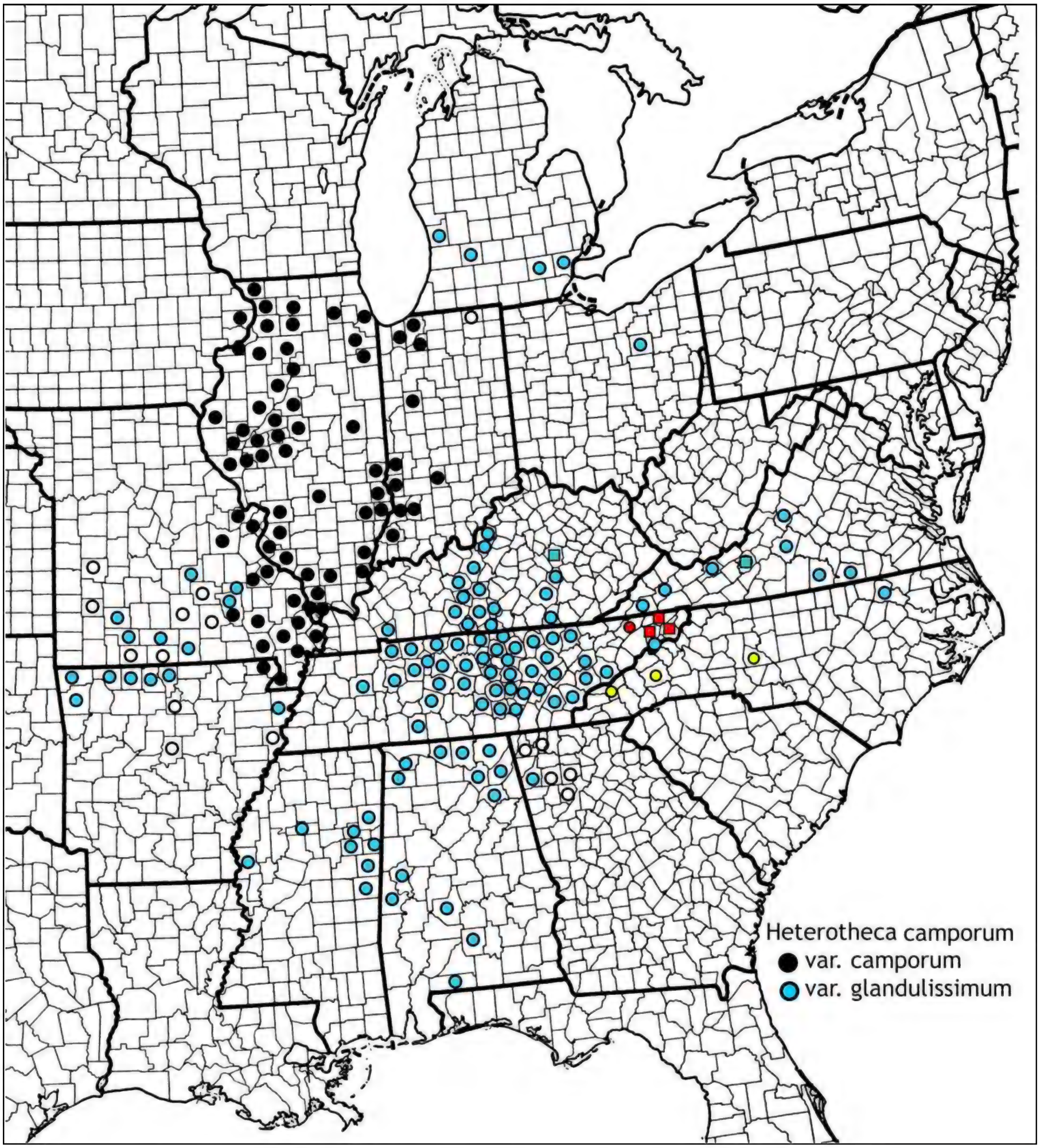

Figure 5. County distribution map of *Heterotheca camporum* var. *camporum* (black) and var. *glandulissima* (blue) (based on Nesom 2020, used by permission) (unfilled dots were specimens not seen by Nesom), showing newly added counties in northeastern Tennessee from current field work (red), and newly added counties in North Carolina from database records (yellow). Squares (three in northeastern Tennessee, one each in Kentucky and Virginia) represent collections from shale substrates.

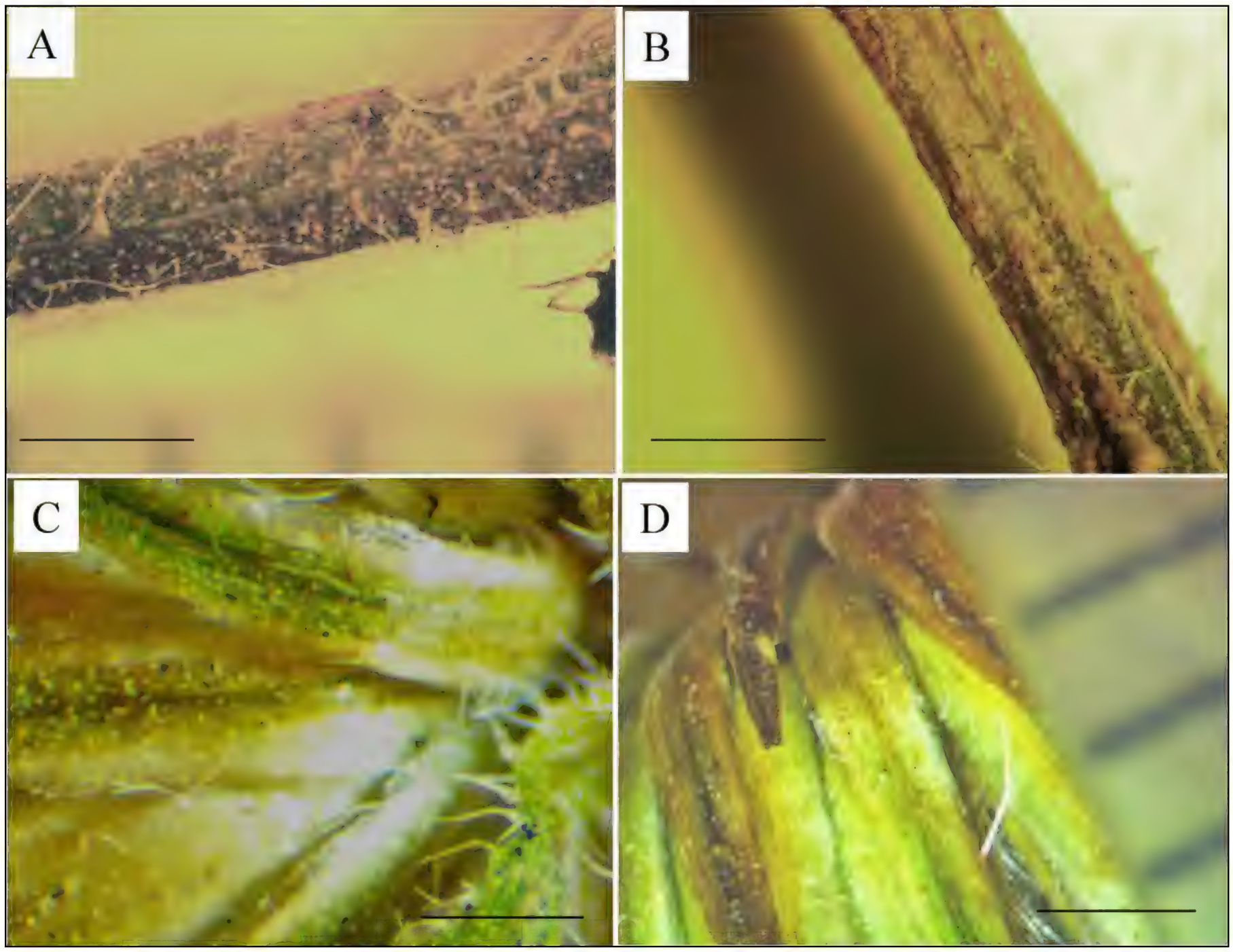

Figure 6. Peduncles with dense (A) or sparse (B) glands and phyllaries with dense (C) or sparse (D) glands. All specimens from northeastern Tennessee, deposited at ETSU and collected by Levy and Walker (A = *20463c*, B = *20466*, C = *20456b*, D = *20466*). Scale bar = 1mm.

Distribution and habitat

Montevallo soils extend far beyond the Booher Knobs region, ranging from Alabama north to Virginia in the Ridge and Valley physiographic province (Soil Web 2020). Although *Heterotheca camporum* var. *glandulissima* has high fidelity to this soil series in the Booher Knobs region and Montevallo soils extend north with little interruption, var. *glandulissima* is regionally rare outside the core knobs area. Similarly, some of the other characteristic Booher Knobs species (*Brickellia eupatorioides* var. *eupatorioides*, *Opuntia humifusa*, *Penstemon brevisepalis*) are largely restricted to the core tri-county area. If these species can be considered bioindicators, there must be a sufficient change in habitat that is not readily apparent from an examination of physiography, soils, and dominant flora. Regardless of the reason for restriction to the Booher Knobs, the rarity of other sites in the region and the scarcity of shale-associated specimens elsewhere suggests an experimental test for of ecotypic differentiation would be worthwhile.

The occurrence of *Heterotheca camporum* var. *glandulissima* at the Holston Army Ammunition Plant in Hawkins County represents a location that would more closely link northeastern Tennessee to the more common locales further south and west and would require less of a long-distance dispersal to reach the knobs. In Virginia, the species has been reported from 8 counties (SERNEC 2020; Virginia Botanical Associates 2020) and has apparently spread rapidly over limestone, dolomite, and disturbed areas in recent decades, especially along the median of I-81 in the Ridge and Valley physiographic region (G. Fleming, pers. comm.). Two specimens from

Montgomery County were associated with shale, one of which is from a "channery soil on hillside" north of Ironto. Ironto is the southern limit of the shale barrens associated with the Brallier shale formation (Wherry 1930; Platt 1951). Based on the label location, this specimen was likely collected from the Berks soil, a channery loam derived from shale. Of the 16 counties in Kentucky with specimens of var. *glandulissima*, the only specimen citing a shale substrate was from Madison County. Although many herbarium specimens lack substrate data, none of the specimens from Alabama, Georgia, North Carolina, and Tennessee (south and west of the study region) listed shale as a substrate but limestone, dolomite, chalk (Alabama), and roadsides were frequently cited.

Nesom (2020) questioned the hypothesis of recent colonization of the eastern part of the range of *Heterotheca camporum* var. *glandulissima*. In a list of habitats in the native geographical range, Nesom (2020) also included shale outcrops along with the more commonly cited limestone, chalk, and roadside occurrences. Moreover, Nesom also noted specimens of eglandular plants collected in Alabama. At Shell Hollow in the knobs, the species was found directly on a naturally-occurring shale outcrop. More information on such potentially natural occurrences is difficult to obtain because there is little public land in the knobs region and undisturbed sites are rare. In the knobs, *Heterotheca camporum* var. *glandulissima* can be abundant over large areas (> 1 ha), but it appears to have very low tolerance of shade or competition. At sites that are more vegetated than rock outcrops or channery shale debris, plants are smaller, less floriferous, and populations are sparser. Therefore the species may be easily eliminated from more fertile and stable sites.

Nesom further suggested that the destruction of the UKT Herbarium by fire in 1934 may explain the absence of Tennessee specimens prior to 1925. However, A. Gattinger, a prolific explorer and collector of the Tennessee flora, especially in the Nashville Basin, left no duplicates of *H. camporum* among the 1407 Tennessee specimens listed on SERNEC and did not include H. *camporum* in his floras (Gattinger 1897, 1901). Albeit negative evidence, this suggests the species was either absent in Tennessee or much rarer compared to modern times.

Morphology

Based on an absence of significant character correlations, the densities of hairs and glands appear independent of each other and the density of each varies independently among plant tissues (stems, peduncles, phyllaries). Further, the densities of glands and hairs were not inversely correlated as might be expected if they were differential responses to different environmental cues. A consequence of this character independence was the observation of population differentiation for phyllary glands, but not for other pubescence or gland characters. Population differentiation suggests there has been sufficient time and isolation among populations for differences to arise; alternatively, there may have been differences among founding propagules of populations or the observation of population differentiation may have been a sampling artifact. The relative degree of uniformity within individuals and within populations argues against the sampling artifact hypothesis.

Morphological character values for stem height, leaf length, and leaf width were congruent with those reported by Semple (1983) (Table 1). For the gland and hair traits that were reported qualitatively by Semple, the density of upper stem glands and phyllary pubescence agreed with Semple's descriptions of "few/many," and "sparse," respectively. However, Semple described peduncle and phyllary glands as "many" but the observations here ranged from few or zero, respectively, to many for each (Fig. 6). Nesom (2020) also noted specimens from Alabama and Mississippi chalk outcrops that were eglandular.

The observations of *Heterotheca camporum* var. *glandulissima* from northeastern Tennessee expand the diversity of preferred habitats and demonstrate a greater degree of morphological variation than previously reported. In northeastern Tennessee, the species appears to have undergone relatively

recent proliferation in the shale belt but with uncertainty surrounding the extent of habitation of natural sites, the time of initial colonization of the region and the shale knobs remains questionable.

Specimens examined (all at ETSU and collected by *Levy and Walker*; * = specimens used in the morphometric analysis). *Heterotheca camporum* var. *glandulissima*. Tennessee. Carter Co.: Rte 19E, E side, ~2 mi S Bunker Hill Rd, Sevier Shale, abundant in open areas, 9 Nov 2020, *20463a–e**; Watauga Dam, N side, 10 Nov 2020, *20465a–c**; Watauga Dam, S side, 10 Nov 2020, *20466**; near upper end of Watauga Dam, on bluffs alongside dam, 8 Oct 2015, *15755*. Hawkins Co.: Holston Army Ammunition Plant, one plant in field in sun; 1/4 mi E main gate, 1/4 mi S Rte 11W, 7 Sep 2019, *19845*; Holston Army Ammunition Plant, ~0.1 mi E of E boundary of HAAP, 0.2 mi NE of water trmnt plant, colony in field with gravel, 29 Sep 2019, *191043*. Sullivan Co.: Piney Flats, Piney Flats Rd, just S of RR crossing, Sevier Shale, abundant around periphery of quarry, 9 Nov 2020 *20463a–c**; Piney Flats Rd just S of RR crossing, 1/2 mi S of Piney Flats Center, old quarry of Sevier Shale, this species has complete fidelity to the Sevier Shale, 30 Aug. 2018, *18355*. Washington Co.: N side East Oakland Ave across from Springbrook Dr, Johnson City, Sevier Shale, old quarry and adjacent area, abundant, 7 Nov 2020, *20456a–d**; N side East Oakland Ave across from Springbrook Dr, Johnson City, Sevier Shale, old quarry and adjacent area, abundant, 8 Nov 2020, *20456a–b**; Cash Hollow, ~1 mi N East Lakeview Dr, Johnson City, Sevier Shale, abundant at old quarry, 8 Nov 2020, *20458a-c**; Cash Hollow, ~1 mi N East Lakeview Dr, Johnson City, Sevier Shale, around landfill, 8 Nov 2020, *20459a-b**; Watauga town, near jct Piney Flats Rd, along RR tracks, 9 Nov 2020, *20460**; Watauga town, 1/4 mi N jct Piney Flats Rd, Sevier Shale, abundant around periphery of quarry, 9 Nov 2020, *20461**; Watauga town, near jct Piney Flats Rd., Sevier Shale, abundant around periphery of quarry, 9 Nov 2020, *20462a–b**; Sevier Shale, above General Shale and Brick near intersect. of Princeton Rd and Oakland Ave, abundant over shale, 26 July 2018, *18263*; near intersect. of Princeton Rd and Oakland Ave, above Toyota dealership, ubiquitous on eroded black shale of Sevier Shale, in sun, 14 Sep 2018, *18377*; Persinger Rd, Sevier Shale belt, disturbed area on shale in sun, absolute fidelity to the shale, 18 Sep 2018, *18383*; Herb Hodge Rd along Watauga River just S of Sullivan Co. line, over shale, plants 4-5' tall, 25 Oct 2018, *18463*.

***Heterotheca subaxillaris*. Tennessee.** Unicoi Co.: Erwin, along RR across from animal shelter near water treatment plant, in sun, many plants, 29 Sep 2015, *15691*; Erwin, W side of RR yard, W side of N Industrial Dr., common at roadside and in RR area, 7 Nov 2020, *20467*, *20468*, *20469*.

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TAXONOMIC REVISION OF *HETEROTHECA* (ASTERACEAE: ASTEREAE): SECT. *PHYLLOTHECA*

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ABSTRACT

A taxonomic revision of the primarily Californian *Heterotheca* sect. *Phyllotheca* recognizes 10 species, including two new ones and several with modified circumscriptions and nomenclature. **Heterotheca sandersii** Nesom, **sp. nov.**, is endemic to a small region of Los Angeles and San Bernardino counties, along the western and southwestern base of the Santa Susana, San Gabriel, and San Bernardino Mountains. **Heterotheca sanctarum** Nesom, **sp. nov.**, is a tetraploid species endemic to Santa Clara, Santa Cruz, San Benito, San Mateo, Contra Costa, and Solano counties — for the most part, it was identified by Semple (1996) within his concept of *H. bolanderi* var. *bolanderioides*. **Heterotheca arenaria** (Elmer) Nesom, **comb. nov.**, has been identified as *H. bolanderi* but is a distinctive coastal strand endemic from Marin Co. northward to Humboldt Co.; *H. bolanderi* sensu stricto is endemic to the hills of Alameda, Contra Costa, Marin, San Mateo, Santa Cruz, and southern Sonoma counties. **Heterotheca** [*Hectorea*] **villosissima** (DC.) Nesom, **comb. nov.**, validates an earlier name for *H. echioides*. *Heterotheca sessiliflora* Nutt. comprises coastal strand populations from northern Baja California and southern San Diego Co., but the type collection was made in Santa Barbara Co. and the species is not currently known in the intervening area. *Heterotheca camphorata*, *H. fastigiata* (without varieties), *H. monarchensis*, and *H. thiniicola* are recognized with justification from morphology and geography.

The taxonomy of sect. *Phyllotheca* follows earlier treatments for sect. *Heterotheca* and *Ammodia* (Phytoneuron 2019-64: 1–44) and sect. *Chrysanthe* (Phytoneuron 2020-68: 1–359). An introduction to the genus and Literature Cited are provided in the first.

HETEROTHECA SECT. PHYLLOTHECA (Nutt.) Harms, Castanea 39: 158. 1974. *Chrysopsis* subg. *Phyllotheca* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 315. 1840. **TYPE**: *Chrysopsis sessiliflora* Nutt. = *Heterotheca sessiliflora* (Nutt.) Shinners.

Hectorea DC., Prodr. 5: 95. 1836. **TYPE**: *Hectorea villosissima* DC. (*Heterotheca villosissima* (DC.) Nesom). See comments regarding *H. bolanderi* and *H. bolanderioides*.

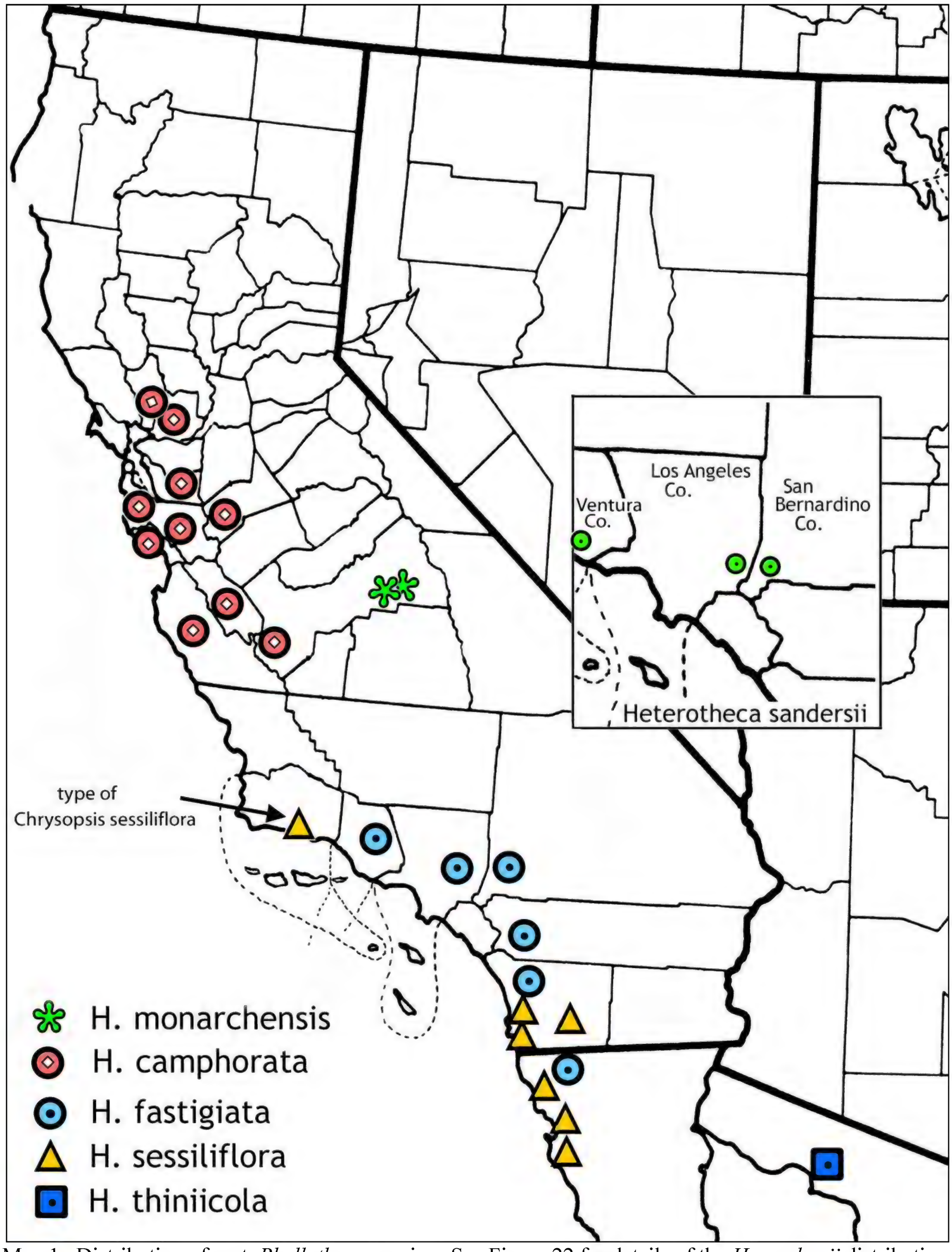
Plants of sect. *Phyllotheca* are distinct in their disc corollas with lobes and often tubes prominently hairy with antrorsely oriented, filiform, multicellular-uniseriate hairs 0.5–2.0 mm long. Variation exists within species and the corolla hairs sometimes are reduced in density or essentially absent. These plants comprise a geographically coherent group of taxa restricted to coastal and near-coastal regions along the Pacific Ocean from Baja California north into central California, with one outlier (*H. thiniicola*) in northwestern Sonora and one (*H. monarchensis*) in the California Sierra. Sect. *Phyllotheca* reasonably might include the species of sect. *Chrysanthe*, which is without clearly defined subgroups. Sects. *Heterotheca* and *Ammodia* each are strongly differentiated.

Apparently there has been little until studies by John Semple toward an explicit rationale for considering the entities of sect. *Phyllotheca* as conspecific — original descriptions of most entities have been at specific rank. Gray (1884) treated the whole group as "var. sessiliflora" within a broadly encompassing concept of *Chrysopsis villosa* — along with all plants/taxa now treated as sect. *Chrysanthe* (i.e., Gray's *Chrysopsis villosa* vars. *canescens*, *echioides*, *foliosa*, *hispida*, *rutteri*,

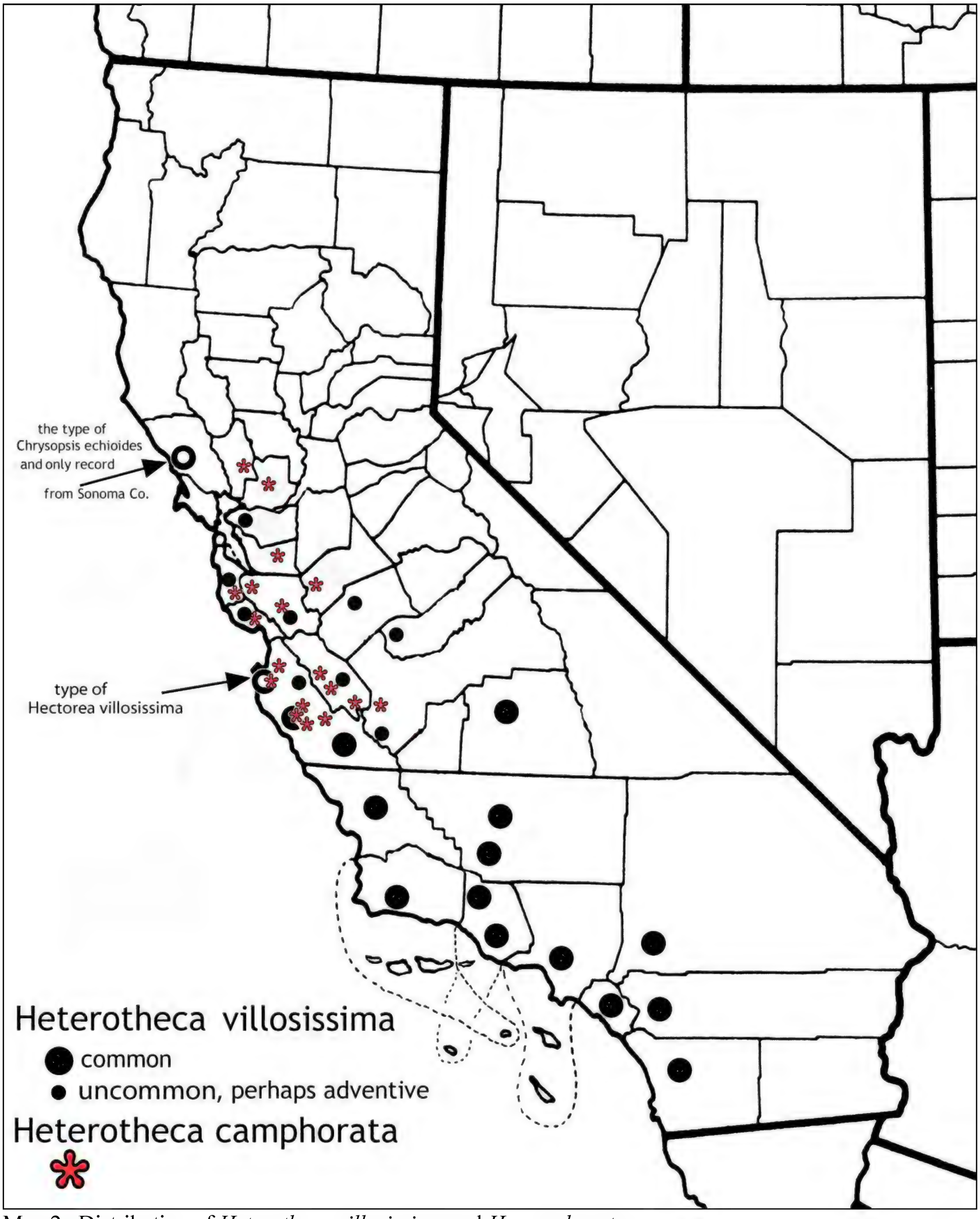
stenophylla, and *viscida*). Hall (1907) and other California botanists followed this course, with caveats: Howell et al. (1958), followed by Harms (1974), treated *Chrysopsis bolanderi* at specific rank; Shinners (1951) recognized *H. echioides* and *H. sessiliflora*; Harms (1974) recognized *H. fastigiata*; Semple (1980) segregated *H. camphorata*. Semple (1992, 2001) consolidated nearly the whole group within the single species *Heterotheca sessiliflora*, keeping at specific rank the more recently described narrow endemics *H. thiniicola* and *H. monarchensis*. Semple's rationale appears to have been substantially based on his working concept of the varietal rank (i.e., treat entities as conspecific varieties if morphologically similar and sympatric). And in 2008 (p. 895) he noted that var. *echioides* functions within his *H. sessiliflora* as a "matrix" taxon by connecting, through hybridization, the entire complex into a single polymorphic species … ."

Semple (1992, 1996) treated *Heterotheca sessiliflora* as comprising subspecies and varieties. *Hectorea villosissima* DC. (1836), however, proves to be the oldest name in sect. *Phyllotheca* and the system of infraspecific ranks set up by Semple within *Heterotheca sessiliflora* Benth. [1840] no longer can be considered correct, even if regarded as biologically appropriate. Semple (1996) cited *Hectorea* DC. as a synonym of *Heterotheca* Cass. but he apparently did not determine the identity of *Hectorea villosissima* (at least he did not cite the species name as a synonym of any other) or consider its nomenclatural significance.

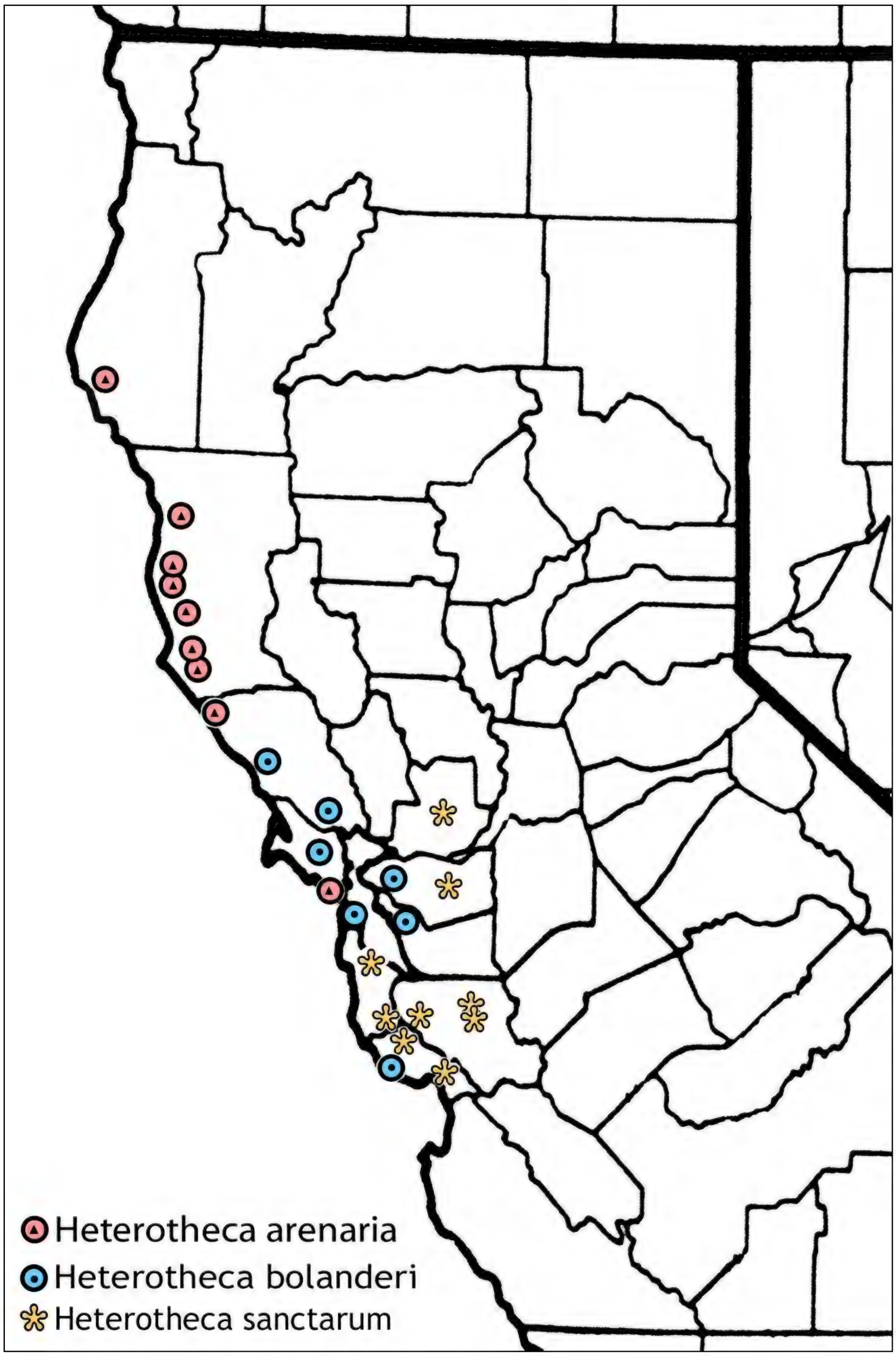
Morphology and geography are interpreted here as supporting recognition of ten species, mostly resolving the biological dissonance of recognizing sympatric conspecific taxa. Morphological criteria for identifying these taxa are generally similar to those in Semple (1996) and other treatments, as discussed below. Nomenclature is significantly modified from previous taxonomy. As with the sect. *Chrysanthe* revision, identifications can be made using maps, illustrations, descriptions, and commentary; key couplets are provided to contrast species pairs, especially those that occur sympatrically.



Map 1. Distribution of sect. *Phyllotheca* species. See Figure 22 for details of the *H. sandersii* distribution.



Map 2. Distribution of *Heterotheca villosissima* and *H. camphorata*.



Map 3. Distribution of *Heterotheca bolanderi* and *H. sanctarum*. See Figure 53 for details of the *H. sanctarum* distribution.

1. **HETEROTHECA MONARCHENSIS** York, Shevock, & Semple in Semple, Rev. Heterotheca Phyllotheca 52, fig. 20. 1996. **TYPE**: **California**. Fresno Co.: Ca. 86 km E of Fresno, Sequoia National Forest, Monarch Wilderness, 2000 m NW of Boyden Cave on N side of Kings River canyon, rocky outcrops, 1800 m, 31 Jul 1995, *D.A. York & J.R. Shevock 109* (holotype: CAS; isotypes: FSC, JEPS, MO, RSA, US, WAT). Type distribution as cited by Semple (1996), neither specimens nor images seen during the present study.

Heterotheca monarchensis is known only from the Monarch Wilderness of Sequoia National Forest in Fresno County, where it occurs on limestone outcrops at about 6000 feet. It is distinct in its small stature (less than 20 cm tall), rhizomatous and mat-forming habit, densely villous-sericeous vestiture giving the plants a silvery green aspect, small, densely overlapping, oblanceolate cauline leaves with broadly undulate margins, and numerous, narrow capitular bracts. Semple (1996) placed it among the species of sect. *Phyllotheca* because of long hairs on the disc corolla lobes and presumably because of its locality in southern California. Leaf morphology has similarities with *H. fastigiata* and *H. villosissima*. Collection images and habit and habitat photos are available (see John Semple's 'Astereae Lab' web page and the USDA Forest Service web page) for the species.

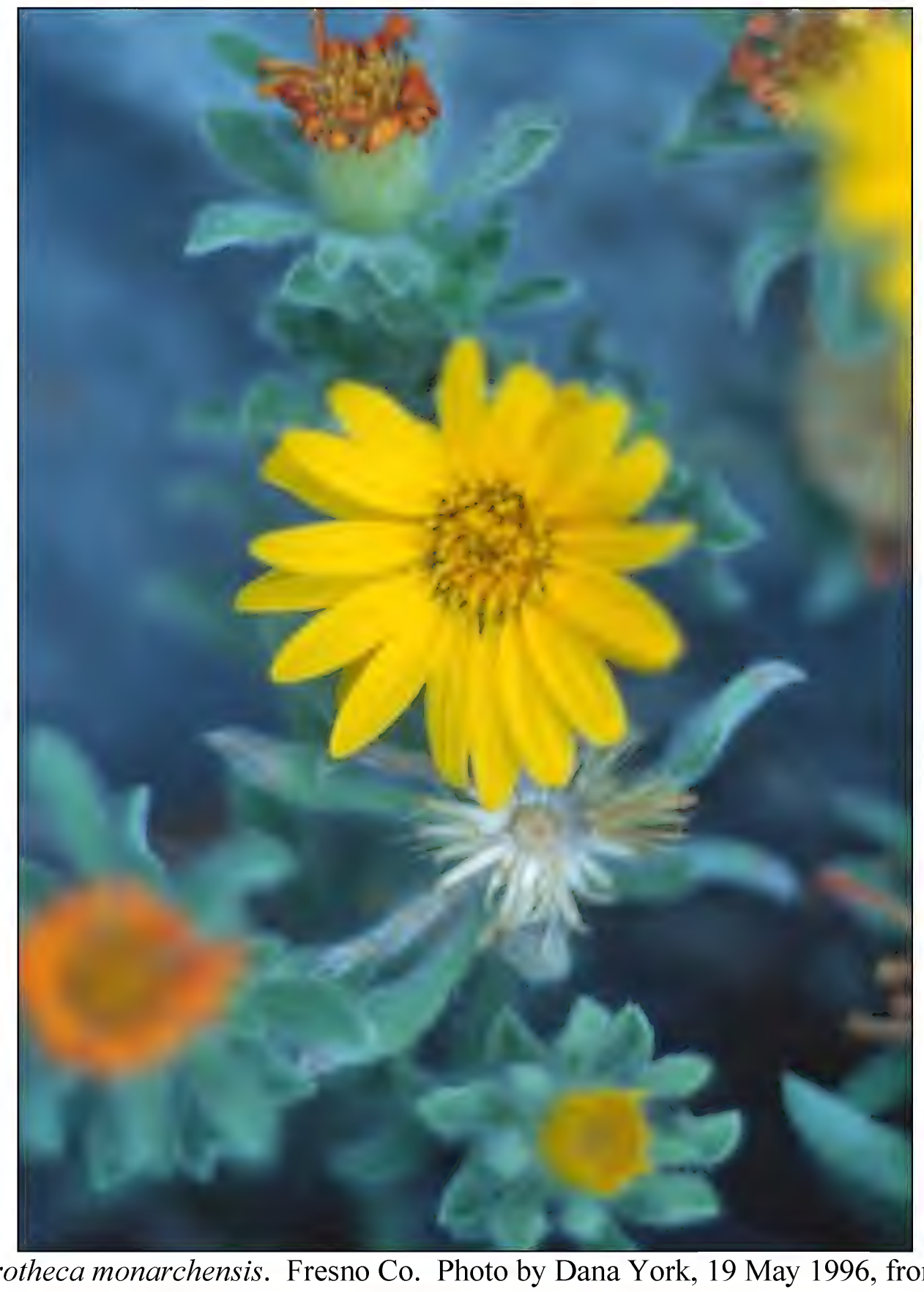


Figure 1. *Heterotheca monarchensis*. Fresno Co. Photo by Dana York, 19 May 1996, from CalPhotos.

2. HETEROTHECA THINIICOLA (Rzed. & Ezc.) B.L. Turner, Phytologia 63: 128. 1987. *Haplopappus thiniicola* Rzed. & Ezc., Cienc. Interamer. 26: 16. 1986. *Heterotheca sessiliflora* var. *thiniicola* (Rzed. & Ezc.) Nesom, Phytologia 83: 17. 1997. **TYPE**: **MEXICO**. **Sonora**. Mpio. Puerto Penasco, Gran Desierto de Alta, 8 km NE de la Estacion Gustavo Sotelo, 17 Dec 1984, *C. Ezcurra 84001* (holotype: MEXU; isotype: TEX!).

Heterotheca thiniicola is similar to *H. fasciculata* in its small, silver-sericeous leaves with wavy margins. Earlier I joined it at varietal rank with *H. sessiliflora* (Nesom 1997) toward consistency with Semple's inclusive taxonomy structure, but the long-disjunct geography of *H. thiniicola* (separated from closest *H. fasciculata* by about 200 miles) and its arid habitat and shrubby habit support its recognition at specific rank, especially in view of the overall taxonomic structure of sect. *Phyllotheca* outlined here.

Figure 2. *Heterotheca thiniicola*. Sonora, *Felger 88-227* (DES).

3. HETEROTHECA FASTIGIATA (Greene) Harms, Brittonia 26: 61. 1974. *Chrysopsis fastigiata* Greene, Pittonia 3: 296. 1898. *Chrysopsis villosa* var. *fastigiata* (Greene) H.M. Hall, Univ. Calif. Publ. Bot. 3: 43. 1907. *Heterotheca sessiliflora* subsp. *fastigiata* (Greene) Semple, Phytologia 73: 451. 1992. *Heterotheca sessiliflora* var. *fastigiata* (Greene) Semple, Rhodora 103: 203. 2001. **TYPE**: **California**. [San Bernadino Co.]: San Bernadino Mts, 1000-1500 ft, 15 Oct 1895, *S.B. Parish 3815* (possible holotype: NDG 53796 image; isotypes: CAS image, GH image, UC not seen, US 652178-Fig. 3, US-2 sheets-Fig. 4).

Semple (1996) cited the NDG specimen as holotype — it has no annotation by Greene but is the only sheet in NDG that fits the protologue.

Heterotheca sessiliflora [subsp. *fastigiata*] var. *sanjacintensis* Semple, Phytologia 73: 452. 1992. **TYPE**: **California**. Riverside Co.: Calif. Hwy 243 just S of Idyllwild Park at Manzanita Drive, 30 Sep 1987, *J.C. Semple 8982* (holotype: WAT; isotypes: CAS-Figs. 5 and 6, NY image, UC!). Semple (1996) also cited isotypes at MT and RSA. *Semple 8981* (OBI), from essentially the same locality, IDed by Semple as var. *sanjacintensis*, 2n = 9II.

Heterotheca fastigiata occurs in northern Baja California (Mpio. Tecate — e.g., Las Juntas, 1887, *Orcutt 9*, MO) and five California counties (San Diego, Riverside, San Bernadino, Los Angeles, Ventura). The plants are characterized by (a) small (5–20 mm long), relatively even-sized, densely overlapping and closely ascending to erect, silvery-sericeous, eglandular cauline leaves with undulate margins, truncate and often subclasping base, and appressed-strigose surfaces and (b) numerous small heads, without closely subtending capitular bracts, on bracteate peduncles (5–15(–30) mm long) in a paniculiform to loosely corymbiform arrangement. Stems are eglandular and puberulent to antrorsely short-strigose, often with a sparse overstory of long, villous hairs. All chromosome count vouchers seen are for diploids: Los Angeles Co.: *Semple 5592*, *Semple & Heard 8629*; Riverside Co.: *Semple & Chmielewski 8981*; San Bernadino Co.: *Semple & Heard 8632, 8978*. Flowering May through November.

Var. *sanjacintensis* as mapped by Semple is nearly congruent in geography with typical *Heterotheca fastigiata* and the specimens he annotated as var. *sanjacintensis* are heterogeneous in morphology. Semple noted that it has leaves "far less densely strigose" ... with "somewhat longer hairs," "the leaves are not nearly as densely pubescent and are more glandular giving them a light green appearance," and in the diagnosis it was compared to typical *E. fastigiata* — geography and apparent continuous variation in density of vestiture suggest that this is populational variation. Analogous variation exists in *H. villosissima* and even the type collection of *H. fastigiata* shows variation in density of vestiture (compare Figs. 3, 4, 5, and 6).

Hybrids are formed between *Heterotheca fastigiata* and *H. villosissima* (pers. observ. and see comment by Semple, 1996, p. 44) where they are sympatric. Much of this may correspond with the elimination of natural habitats and the widespread creation of hybrid ones.

1. Stems usually branching distally above a long, unbranched section, inflorescence usually compact; leaves small, densely overlapping, erect and appressed against the stem, margins wavy, eciliate or weakly so proximally, surfaces silvery- to gray-sericeous with closely set hairs; heads without capitular bracts; ray ligules mostly 3.5–6 mm long ..... **Heterotheca fastigiata**

1. Stems usually branching from midstem to distally, inflorescence looser and more elongate; leaves larger, slightly overlapping, usually distinctly spreading, margins wavy or not, long-ciliate proximally, surfaces greenish with reduced vestiture to loosely silvery-sericeous with denser vestiture; heads usually with short capitular bracts, sometimes without; ray ligules mostly 5.5–10 mm long ..... **Heterotheca villosissima**

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 3. *Heterotheca fastigiata*. Isotype (US 652178) of *Chrysopsis fastigiata*.

Figure 4. *Heterotheca fastigiata*. Isotype (US 1682282) of *Chrysopsis fastigiata*.

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 5. *Heterotheca fastigiata*. Isotype of *H. sessiliflora* var. *sanjacintensis* (CAS).

Figure 6. *Heterotheca fastigiata*. Detail from isotype (NY) of *Heterotheca sessiliflora* var. *sanjacintensis*.

Figure 7. *Heterotheca fastigiata*. Ventura Co., *Pollard s.n.* (NO).

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 8. *Heterotheca fastigiata*. San Bernardino Co., *Semple & Heard 8632* (GA).

4. HETEROTHECA VILLOSISSIMA (DC.) Nesom, **comb. nov.** *Hectorea villosissima* DC., Prodr. 5: 95. 1836. **TYPE**: Protologue: [MEXICO. Hidalgo]. "Prope Real del Monte legit cl.| Haenke" but see comments below. Probably: **USA**. **California**. Monterey Co.: Vicinity of Monterey, 1793, *T. Haenke s.n.* (holotype: G-DC, Fig. 9).

Thaddäus Haenke was Naturalist-Botanist of the Malaspina Expedition of 1790-1793, which explored South America to Central America, California (the Monterrey area), and Alaska and westward to the southwestern Pacific region (see Wikipedia for T. Haenke and the Malaspina Expedition). The type specimen of *Hectorea villosissima* clearly is a *Heterotheca* but there is no species like it in Hidalgo, Mexico, where the protologue indicates the collection was made, or even anywhere in Mexico. Instead, it is a plant of the species previously identified as *Heterotheca echioides*, which does occur in the area of Monterey, California, where the Malaspina Expedition stopped in 1793 (Monterey was its only stopping place in California). A packet affixed to the G-DC specimen notes "Mexiq. Haenke" but this and the protologue surely do not describe the actual collection locality. De Candolle's protologue description fits the Haenke specimen, and Asa Gray annotated the *Hectorea villosissima* type in 1887 as *Heterotheca echioides*.

Chrysopsis echioides Benth., Bot. Voy. Sulphur, 25. 1844. *Chrysopsis villosa* var. *echioides* (Benth.) A. Gray, Synopt. Fl. N. Amer. 23(1): 123. 1884. *Heterotheca echioides* (Benth.) Shinners, Field & Lab. 19: 71. 1951. *Heterotheca sessiliflora* subsp. *echioides* (Shinners) Semple, Phytologia 73: 450. 1992. *Heterotheca sessiliflora* var. *echioides* (Benth.) Semple, Rhodora 103: 203. 2001. **TYPE**: **California**. [Sonoma Co.]: Bodegas, 1841, *R.B. Hinds s.n.* (holotype: K-Fig. 10, fragment US! and specimen photo US!-mounted on the sheet with the fragment). Hinds was at Bodega Bay in Sep 1839, fide Raven (1964).

The type collection of *Heterotheca echioides* ("Bodegas," presumably Bodega Bay in Sonoma Co.; Map 2) was made north of the known range of the species (= *H. villosissima*). Only two specimens identified as *H. echioides* (or var. *echioides*, subsp. *echioides*) from Sonoma County have been included in the California Consortium database (as seen in 2015, 2016) — *Howell 5342*, 13 Jul 1930 (POM); *Rubtzoff 8329*, 16 Aug 1975 (CAS) — both collections, however, are correctly identified as *H. bolanderi* (pers. observ.). The only locality of *H. echioides* mapped by Semple (1996) in Sonoma County is Bodega Bay, presumably representing the type, as he cited no other collection from Sonoma County. The only species of sect. *Phyllotheca* currently known in Sonoma County are *H. arenaria* and *H. bolanderi*, and the Hinds collection is distinctly different from both species.

Chrysopsis californica Elmer, Bot. Gaz. 39: 48. 1905. **TYPE**: **California**. Santa Barbara Co.: Gaviota, [protologue: "sandy soil near beach"], May 1902, *A.D.E. Elmer 4148* (holotype: DS!; isotypes: MIN image, MO!, US-Fig. 13). The type is a silvery-sericeous plant with small capitular bracts — very similar in aspect to the type of *Hectorea villosissima*.

Leaves of *Heterotheca villosissima* sometimes are gray to silvery in aspect (like *H. fastigiata*) with densely villous to pilose-villous vestiture, but more characteristic vestiture is less dense and the surfaces more greenish, sometimes hirsute; proximal margins are long-ciliate; base usually narrowed, attenuate to rounded and usually subclasping. Stems eglandular and hirsute-pilose to hirsute-villous with thin, spreading to slightly deflexed hairs; phyllaries are glandular and villous with fine hairs. Cauline leaves usually are not densely overlapping and axillary tufts of small leaves are characteristic, these often lengthening into lateral branches. Capitular bracts usually are present, commonly about 1/3–1/2 the involucre length; they sometimes are absent or even more reduced in size, perhaps reflecting gene flow from *H. fastigiata* (where sympatric). Numerous chromosome counts by Semple (fide label data) document only diploids in *H. villosissima* — from Kern, Fresno, Monterey, San Bernadino, San Luis Obispo, Santa Barbara, and Ventura counties.

A collection from southern Oregon, far out of range and perhaps a waif, is tentatively identified here as *Heterotheca villosissima*: Jackson Co.: Dead Indian Mem. Road, 2 mi E of Emigrant Creek bridge, gravelly, grassy disturbed roadside, 2150 ft, 23 Jul 2005, *Duncan 3026* (SOC, Fig. 21).

Contrasts of *Heterotheca villosissima* with *H. fastigiata*, *H. bolanderi*, and *H. sessiliflora* are given in key couplets following each of the latter species.

Figure 9. *Hectorea villosissima* DC., holotype (G-DC), probably from the vicinity of Monterey, California (see text). Small capitular bracts present.

Figure 10. *Chrysopsis echioides*, the type collection (K) from Sonoma Co., California, placed here as a synonym of *Heterotheca villosissima*. Collected north of the currently known range of the species but the morphology is that of *H. villosissima* — see comments in text. Small capitular bracts present.

Figure 11. *Heterotheca villosissima*. Monterey Co., *Elmer 3393* (US). Capitular bracts present.

Figure 12. *Heterotheca villosissima*. Monterey Co., *Ewan 9171* (NO). Capitular bracts present. Vestiture similar to that of the *Hectorea villosissima* type (Fig. 9). Unusually long peduncles with reduced bracts, perhaps resulting from proximal stem damage.

Figure 13. *Heterotheca villosissima*. Santa Barbara Co., isotype of *Chrysopsis californica* (US). Capitular bracts present.

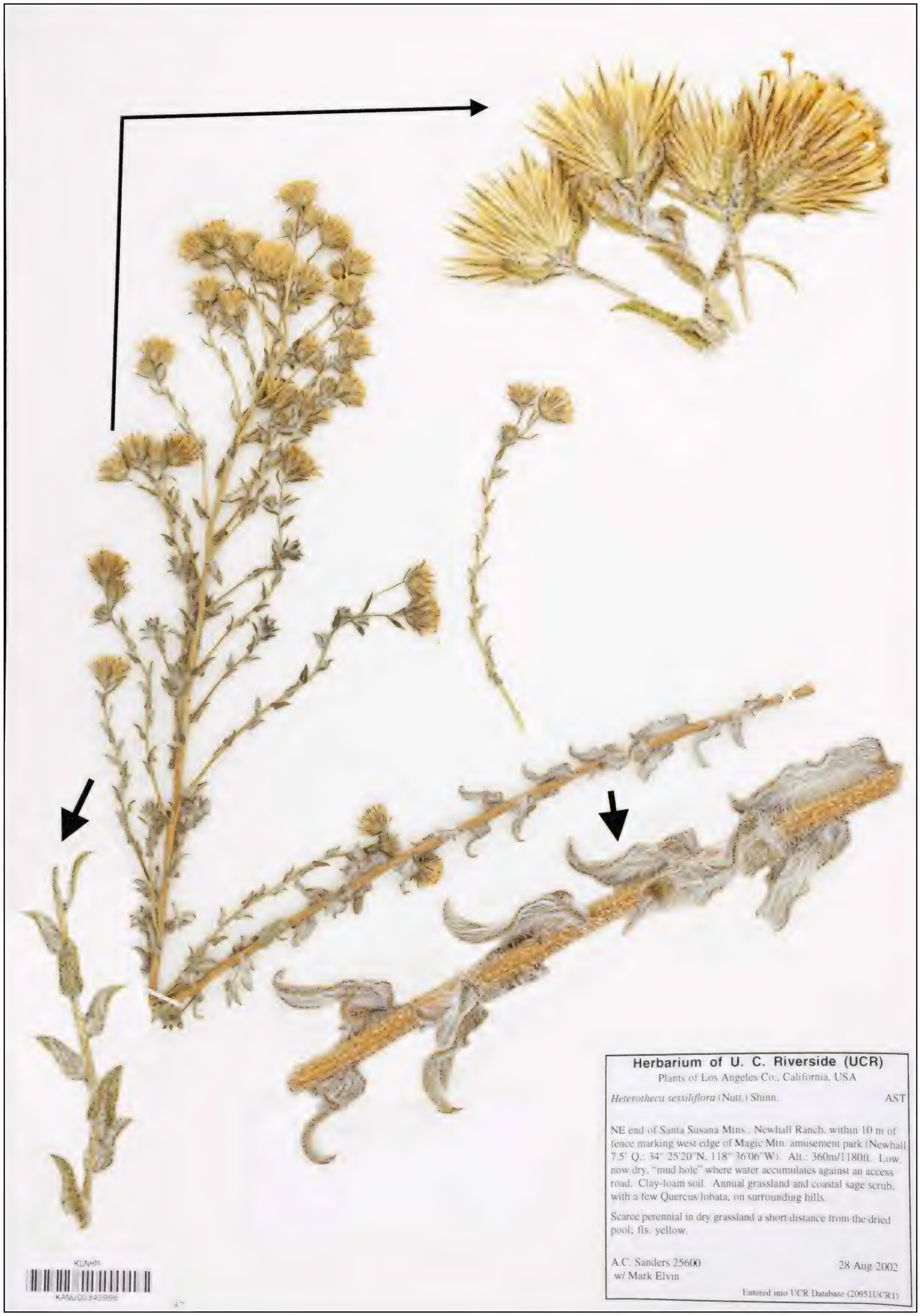


Figure 14. *Heterotheca villosissima*. Los Angeles Co., *Sanders 25600* (KANU). Capitular bracts present.

Figure 15. *Heterotheca villosissima*. Los Angeles Co., *Cromwell s.n.* (APSC). Capitular bracts apparently absent or few.

Figure 16. *Heterotheca villosissima*, perhaps with genetic influence of *H. fastigiata*. Los Angeles Co., *Braunton 706* (US). Capitular bracts apparently absent.

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 17. *Heterotheca villosissima*. Riverside Co., *Roos s.n.* (GSW). Small capitular bracts variably present.

Figure 18. *Heterotheca villosissima*. Riverside Co., *Sanders 35,894* (BRY). Capitular bracts present.

Figure 19. *Heterotheca villosissima*. San Diego Co., *Lauri 371* (SDSU). Capitular bracts present.

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 20. *Heterotheca villosissima*. San Bernardino Co., *Bell 11,190* (RSA). Capitular bracts present.

Figure 21. *Heterotheca* aff. *villosissima*. Jackson Co., Oregon, *Duncan 3026* (SOC). See text (p. 16).

5. HETEROTHECA SANDERSII Nesom, **sp. nov. TYPE**: **California**. Los Angeles Co.: San Gabriel Mts, mouth of Burro Canyon near the confluence of the E and W Forks of the San Gabriel River, ca. 1460 ft (stream bottom) to 1530 ft (slopes), locally common biennial/short-lived perennial on disturbed flats, 20 Jun 1990, *T. Ross 3589* with Fritsch (holotype: RSA!; isotype: UC-Fig. 23).

Distinctive in its heads without capitular bracts, on long, naked or few-bracteate peduncles in loosely paniculate clusters, strongly keeled phyllaries, dark green, hirsute to hirsute-villous leaf and stem surfaces not obscured by vestiture, herbage drying with a dark cast, and stems densely and evenly stipitate-glandular, without eglandular hairs or also sparsely hirsute to villous with spreading hairs. Different from *H. fastigiata* in its dark green, hirsute to hirsute-villous stems and leaves, glandular stems, and keeled phyllaries. Different from *H. villosissima* in its densely stipitate-glandular stems, essentially eciliate leaf and bract margins, longer peduncles, lack of capitular bracts, and prominently keeled phyllaries.

Short-lived perennial herbs from a woody taproot. **Stems** erect, mostly 20–60 cm tall, densely and evenly stipitate-glandular, without eglandular hairs or also sparsely hirsute to villous with spreading hairs. **Leaves** densely arranged and overlapping proximally, more widely spaced distally, mostly oblong to oblong-lanceolate, (10–)15–30(–40) mm long, 3–8(–10) mm wide, bases of proximal subclasping, becoming non-clasping distally, margins eciliate or sometimes with a few weak cilia proximally, not undulate, surfaces hirsute to hirsute-villous, eglandular or minutely and inconspicuously glandular. **Heads** in loosely paniculate clusters, more or less solitary on long (2.5–9 cm), naked or few-bracteate peduncles, peduncular bracts 15–40(–55) mm long, flowering branches from proximal to distal nodes; involucres campanulate, 8–15 mm wide, 7–10 mm long; phyllaries linear-lanceolate, in 4–5 series strongly graduate in length, inner 7–10 mm long, outermost ca. 1/3–1/5 the inner length, inner to outer strongly keeled with a narrow, raised, indurate midregion, distal 1/3–1/2 green except for indurate margins. **Ray flowers** 12–16. **Disc corollas** minutely strigose-villous with fragile hairs near the tube-throat junction and a few longer hairs from near the base of the lobes. **Achenes** 3–4 mm long, densely strigose; pappus bristles longer than the disc corollas.

Alluvial slopes and benches, sandy flats, roadsides, 450–1550 ft; flowering Mar-Aug. *Heterotheca sandersii* is named for Dr. Andrew Sanders, Curator of the UCR Herbarium and a long-time student of the Californian flora.

Additional collections examined. **California**. Los Angeles Co.: San Gabriel Canyon, 1 mi above dam, from 0.5 mi below dam to 1.0 mi above, 1300-1600 ft, 18 May 1936, *Clokey & Templeton 5666* (JEPS, RENO image, RSA, SMU, UC, UCR; and as cited by Semple, CAN, KANU, NY-2, WTU); Claremont, roadside, 1200 ft, 22 Apr 1921, *Cowles 4482* (POM; San Gabriel Valley, S of Santa Fe Dam along E side of Live Oak Lane, 0.6 km SE of intersct I-605 and Arrow Hwy, 128 m, rare, disturbed roadside among weedy species and grasses, 4 May 2010, *Parikh and Gale 3144* (UCR); Lady Bug Canyon, Angeles Crest Hwy, 2 Sep 1937, *Ramsey 163* (POM); NE end of Santa Susana Mts, Newhall Ranch, Santa Clara River bed, below confluence of Castaic Creek, E of Del Valle, 920 ft, riparian forest and open sandy areas below bluffs on S side of river, scarce perennial in dry sand on open flats, 6 Aug 2003, *Sanders 27138* (RSA, UCR); San Gabriel Valley, San Gabriel River channel between Ramona Blvd and Lower Azusa Rd, SW lobe of Irwindale between Baldwin Park and El Monte, under SCE powerlines, channelized river between rock berms, vegetation periodically cut and thinned, fairly common perennial on open, sandy flats in channel, 28 May 2009, *Sanders 37011* (UCR); San Gabriel Valley, W edge of I-605 and ca. 1 mi W of the center of the Santa Fe Flood Control Basin, N of Arrow Hwy and S of Duarte, 460 ft, alluvial slope with remnant patch of brushy sage scrub with chaparral elements, scarce perennial in open, disturbed area, 1 Jun 2009, *Sanders 37081B* (UCR); Pasadena, Arroyo Seco, 30 Aug 2003, *Wilcox s.n.* (UCR). San Bernardino Co.: San Bernardino Natl Forest, 1.6 air mi NNE of Cajon Jct, localized population in open area beside Cajon Pass railway tracks, post-fire surveys on the Blue Cut Fire of 2016, 27 Jun 2017, *Bell 11,109* (RSA); Ontario, Etiwanda Wash [E. Etiwanda Creek], SW corner of Etiwanda Ave and 4th St/San Bernardino Rd, 1030 ft, dry sandy wash with sparsely distributed "islands' of vegetation, 12 Mar 1998, *Provance 182* (UCR); Santa Ana River wash, W side of the Riverside Drive/Main St. bridge, from under the bridge to ca. 0.25 mi W of it, 800-820 ft, uncommon perennial, open areas on sandy benches, 5 Aug 2000, *Provance 2180* (UCR); Colton, Santa Ana River from

Riverside Ave. (N. Main St.) bridge downstream to Riverside County line, disturbed riparian zone in sandy river bottom, with *Salix*, *Baccharis salicifolia*, etc., 820 ft, 28 Jul 1994, *Sanders 15189* (RSA, UCR, UTEP, not seen); Agua Mansa area, N side of the Santa Ana River just E of Riverside Ave, 850 ft, disturbed riparian forest at site of old horse show facility, scarce perennial on sandy bench near the river, 28 May 1998, *Sanders 21877* (TEX); San Bernardino Valley, Santa Ana River floodplain SE of East Highlands, pipeline route from Cone Camp Rd toward Mentone, between Greenspot Rd and the main channel, 1550 ft, coarse sandy and gravelly soil with stones and boulders, sage scrub with chaparral elements, uncommon perennial in dry open sites, 5 Jun 2006, *Sanders 33098* (UCR). Ventura Co.: Donton property (Nature Conservancy) along Santa Clara River from E of the 101 freeway, bridge between Ventura and Oxnard, open wash, 54-60 ft, 31 Mar 2015, *Gross et al. 6910a* (RSA).

1. Heads on long, ebracteate or bracteate peduncles, without capitular bracts; stems densely and evenly stipitate-glandular stems and leaves often drying with a distinctly dark cast; all phyllaries (inner to outer) prominently keeled ..... **Heterotheca sandersii**
1. Heads on sparsely to densely leafy stems, usually with small capitular bracts; stems usually eglandular or minutely glandular; stems and leaves drying greenish to silvery-gray, without a dark cast; phyllaries not keeled or just the inner proximally ..... **Heterotheca villosissima**

The geographic range of *Heterotheca sandersii* is small and most of the known localities are essentially in urban areas (three are in the Angeles National Forest, in San Gabriel and Lady Bug canyons) — all are along the western and southwestern base of the Santa Susana, San Gabriel, and San Bernardino Mountains (Fig. 22). The habitats are mostly alluvial and associated with (from west to east) Arroyo Seco, the Santa Clara River, San Gabriel River, East Etiwanda Creek, and Santa Ana River.

Figure 22. Distribution of *Heterotheca sandersii*. Localities mapped here are in Los Angeles and San Bernardino counties. The collection from Ventura Co. (see Map 1) is not shown at the smaller scale here, perhaps a waif transported downstream along the Santa Clara River.

Heterotheca sandersii is unusual enough in appearance that collectors have speculated that the plants might be hybrids between *H. grandiflora* and *H. sessiliflora* (sensu lato) (see labels for *Sanders 37011*, *37081B*; *Provance 2180*), perhaps because of the dark-drying herbage and the relatively large heads with distinctly keeled phyllaries. The achenes, however, are not dimorphic (as in *H. grandiflora*) and the numerous collections with coherent geography suggest that *H. sandersii* is a stable entity. A chromosome count has not been made.

Heterotheca sandersii has been collected in close proximity to *H. fastigiata* at the northeastern end of the Santa Susana Mountains, in San Gabriel Canyon and at lower elevations along the San Gabriel and Santa Ana rivers, and along the Etiwanda Creek Wash.

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 23. *Heterotheca sandersii*. Los Angeles Co., isotype (UC).

Figure 24. *Heterotheca sandersii*. Los Angeles Co., *Sanders 37081B* (UCR).

Figure 25. *Heterotheca sandersii*. San Bernardino Co., *Sanders 33098* (UCR).

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 26. *Heterotheca sandersii*. San Bernardino Co., *Bell 11,109* (RSA).

Figure 27. *Heterotheca sandersii*. Los Angeles Co., *Clokey & Templeton 5666* (RENO). Middle two heads are at anthesis, others pre-anthesis with still lengthening peduncles.

6. HETEROTHECA SESSILIFLORA (Nutt.) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis sessiliflora* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 317. 1840. *Chrysopsis villosa* var. *sessiliflora* (Nutt.) A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. **TYPE**: **California**. [Santa Barbara Co.]: Protologue: "St. Barbara, Upper California. Flowering in April," 1836, *T. Nuttall s.n.* (holotype: BM, Fig. 28; isotype: GH image, detail Fig. 29).

Handwritten labels by Nuttall on the holotype and the isotype specify Santa Barbara as the collection locality (the BM sheet has 3 labels, each apparently separately written by Nuttall).

Plants often subshrubby, forming colonies from rhizomes or rooting caudices. **Stems** ascending, up to 100(–130) cm high, sessile-glandular, moderately to densely villous to hirsute-villous or pilose-hirsute, less commonly hirsutulous, hairs spreading to loosely antrorsely appressed. **Leaves** basal and cauline; basal usually shed by flowering; cauline usually closely overlapping, broadly oblong to oblong-ovate, base truncate and sessile to truncate-rounded and subclasping, apex rounded to acute, margins straight or undulate, surfaces densely and evenly minutely sessile-glandular (orange), the glands mostly obscured by the dense, loosely villous-strigose to hirsutulous vestiture. **Heads** relatively few in a corymbiform arrangement, with narrow capitular bracts equalling or longer than the involucre and with spreading-ciliate margins; involucres 13–22 mm wide; phyllaries glandular and moderately strigose, at least distally. **Ray flowers** ca. 15–30. Chromosome number, $2n = 18$ (*Semple & Chmielewski 8991*). Figures 28-36.

Representative collections examined. **MEXICO**. **Baja California**. Descanso, dunes, 5 Apr 1949, *Higgins & Harbison s.n.* (DS); Playas De Rosarito, just S of El Descanso, common on inner slope of dunes, some with *Het. grandiflora*, bushy, ca. 1 m high, 8 May 1977, *Moran 24002* (ARIZ, DES, RSA, UCR); near mouth of Rio San Miguel, W of La Mision, local in dunes, 29 Apr 1972, *Moran 19118* (ASU, CAS); Ensenada, sand dunes, 16 Oct 1936, *Rose 36758* (CAS); Tia Juana, 1912, *Smith 5203* (US); 2 mi N of Rosarito Beach, landward margin of sand dunes, 7 Sep 1929, *Wiggins & Gillespie 3877* (CAS, DS, US); ca. 13 mi S of Tijuana near road to Ensenada, 27 Jun 1962, *Wiggins & Thomas 342* (DS). **USA. California**. San Diego Co. (native range): Ocean Beach near San Diego, Oct 1906, *K. Brandegee s.n.* (RENO, RSA); S San Diego, 3 Oct 1903, *Chandler 4117* (DS); Silver Strand Beach State Park, stabilized sand dunes, 30 Aug 1932, *Demaree 9308* (US); Tijuana River, 8 Aug 1902, *Herre s.n.* (DS); near National Monument, SW corner of U.S., 11 Jun 1928, *Johnson s.n.* (CAS); Silver Strand, partially stabilized areas on the sand dunes, 19 Sep 1933, *Purer 5565* (DS); Del Mar, hills S of racetrack near Torrey Pines Woodland, N-facing slope at mouth of steep drainage, 2 Jul 1988, *Reiser s.n.* (SD); Torrey Pines beach, dry sandy flats behind beach, with [*Isocoma*], 15 ft, 19 Aug 1950, *Roos 4938*[a] (DS, GH, UC); Torrey Pines Park, matted perennial at edge of salt marsh with *Baccharis viminea* 19 Aug 1950, *Roos 4938*[b] (RSA); San Diego, CA-75, Imperial Beach and Silver Strand State Beach, just N of S entrance to CA-75, 1 Oct 1987, *Semple & Chmielewski 8991*, voucher for $2n = 18$ (GH, NY, RSA); vicinity of San Diego, 1 m high, dry slopes, 200 ft, 8 Sep 1916, *Spencer 77* (US); Crown Pt., near Pacific Beach, 24 Aug 1933, *Youngberg 2844* SDSU-2 sheets). San Diego Co. (probably a waif): Pine Valley, [ca. 3700 ft], 12 Aug 1894, *Mearns 3976* (US, Fig. 36).

Heterotheca sessiliflora is distinct in its colonial habit, tall stems, broadly oblong, usually closely overlapping cauline leaves with glandular surfaces obscured or not by non-glandular hairs of variable density, and relatively large heads consistently subtended by capitular bracts equalling or longer than the involucre. It is endemic to coastal strand habitats in the southern half of San Diego Co. and a roughly equivalent area along the coast of northwestern Baja California. The type of *H. sessiliflora*, however, was collected in Santa Barbara Co., north of the currently known range of the species.

The inland plant collected by Edgar Mearns at Pine Valley in 1894 (Fig. 36) probably was a waif there or was perhaps even established from a garden planting. At the time, there was gold mining in Pine Valley and presumably an active connection between there and the San Diego area.

Over the course of the present study, I identified collections of typical *Heterotheca sessiliflora* using the epithet "litorea" in attempt to account for the geographical discrepancy of the type collection, but that solution proved to be no less problematic.

Figure 28. *Heterotheca sessiliflora*, the type from BM, *Nuttall s.n.* from Santa Barbara in 1836.

Figure 29. *Heterotheca sessiliflora*, detail from GH isotype.

Figure 30. *Heterotheca sessiliflora*, from dunes just south of of El Descanso, Baja California. Details from *Moran 24002* (DES).

Figure 31. *Heterotheca sessiliflora,* near Torrey Pines, San Diego Co. *Reiser s.n.* (SD).

Figure 32. *Heterotheca sessiliflora*, Crown Point, San Diego Co. *Youngberg s.n.* (SDSU).

Figure 33. *Heterotheca sessiliflora*, Silver Strand Beach, San Diego Co. *Demaree 9308* (US).

Figure 34. *Heterotheca sessiliflora*, Ocean Beach, San Diego Co. *K. Brandegee s.n.* (RENO).

Figure 35. *Heterotheca sessiliflora*, Baja California. *Moran 19118* (ASU). Nonglandular vestiture unusually dense.

Figure 36. *Heterotheca sessiliflora*, Pine Valley in 1894, San Diego County. *Mearns 3976* (US). Probably a waif at this locality (see text, p. 35).

Apparently because of its seaside habitat, typical *Heterotheca sessiliflora* apparently is not sympatric with other species of the section. *Heterotheca villosissima* is distinct from *H. sessiliflora* in its smaller and solitary/caespitose habit, narrower, less congested cauline leaves, characteristically less dense vestiture and reduced glandularity of the leaf surfaces, more elongate capitulescence, and smaller and fewer capitular bracts (if present).

7. HETEROTHECA CAMPHORATA (Eastw.) Semple, Canad. J. Bot. 58: 148. 1980. *Chrysopsis camphorata* Eastw., Zöe 5: 81. 1900. *Chrysopsis villosa* var. *camphorata* (Eastw.) Jeps., Man. Fl. Pl. Calif., 1036. 1925. *Heterotheca sessiliflora* var. *camphorata* (Eastw.) Semple, Phytologia 73: 451. 1992. **TYPE**: **California**. Santa Cruz Co.: Glenwood, Jul 1900, *H. Davis s.n.* (holotype: CAS; isotypes: DS, GH, NY, RM-3 sheets! images, UC, US-Fig. 37).

Chrysopsis vestita Greene in Baker, W. Amer. Pl. 1: 8. 1902. **TYPE**: **USA**. **California**. Santa Clara Co.: Palo Alto, occasional near the marshes, 15 Sep 1902, *C.F. Baker 1670* (holotype: US, Fig. 38; isotypes: GH image, K image, LL! image, MO!, POM, NY, UC). POM, NY, and UC as cited by Semple.

Semple's isotype annotation labels say "Holotype at NDG, not seen" but (fide Barbara Hellenthal, pers. comm. 2016) there is no specimen of this in NDG.

Heterotheca camphorata is characterized by its minutely but prominently sessile-glandular to short-stipitate-glandular and otherwise sparsely hispid-pilose to hirsute-villous upper stems, leaves, and capitulescence, or the stems may lack non-glandular hairs. Heads are on bracteate peduncles; capitular bracts are absent or small and inconsistently present. The species is known from a cluster of 9 counties (Maps 1, 2; uncommon in Napa and Solano cos.) and is abundantly represented by collections — it is not often misidentified. It is sympatric with *H. sanctarum* (tetraploid; unambiguous hybrids not seen but possibly present, see below) and *H. villosissima* (diploid; apparent hybrids and introgressants occur).

Semple (1996, p. 46) noted that diploids and tetraploids occur within *Heterotheca camphorata* and that ploidy level does not appear to be correlated with variation in head size. The only vouchers I have seen, however, are for diploid counts: Fresno Co.: *Semple 8944*; Monterey Co.: *Semple 8932*, *8933*, 8934, *8937*, *8938*, *Semple 8603*, *8606*; Santa Clara Co.: *Semple 8922*, *8923*; Santa Cruz Co.: *Semple 5668*, *Semple 8920*, *Semple 8597*. Semple's tetraploid counts (see Semple 2008: *Semple 8924, Semple 8926*) are from the Mt. Hamilton area in Santa Clara Co., involving plants identified here as *H. sanctarum* (4x) and apparent hybrids between it and *H. camphorata*.

Heterotheca camphorata was treated as *H. sessiliflora* var. *camphorata* by Semple in 1996, but subsequent treatments (Semple in FNANM 2006 and in the Jepson Flora 2012) recognized it less formally. In 2006, Semple listed var. *camphorata* only as a synonym of subsp. *echioides* but referred to it as distinct in his subsequent comments. Similarly, he noted in 2012 that "densely glandular plants [of *H. sessiliflora* subsp. *echioides*] from southern SnFrB, northern SCo with ± glabrous disk corolla lobes may be treated as *Hetherotheca sessiliflora* var. *camphorata* (Eastw.) Semple."

Figure 37. *Heterotheca camphorata*, Santa Cruz County. Isotype of *Chrysopis camphorata* (US). Stems sessile- to short-stipitate-glandular, without non-glandular hairs.

Figure 38. *Heterotheca camphorata*, Santa Clara County. Isotype of *Chrysopis vestita* (US). Stems sparsely hirsute with non-glandular hairs, perhaps reflecting gene flow from *H. villosissima*.

8. HETEROTHECA BOLANDERI (A. Gray) Harms, Brittonia 26: 61. 1974. *Chrysopsis bolanderi* A. Gray, Proc. Amer. Acad. Arts 6: 543. 1866. *Chrysopsis villosa* var. *bolanderi* (A. Gray) A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. *Heterotheca echioides* var. *bolanderi* (A. Gray) Nesom, Phytologia 83: 17. 1997. **TYPE**: **California**. [Alameda Co.]: Oakland Hills, near San Francisco, 1863, *H.N. Bolander 2466* (holotype: GH image; isotypes: K, US image, YU image).

Heterotheca sessiliflora var. *bolanderioides* Semple, Phytologia 73: 450. 1992. *Heterotheca echioides* var. *bolanderioides* (Semple) Nesom, Phytologia 83: 17. 1997. **TYPE**: **California**. Contra Costa Co.: Charles Tilden Regional Park, Vollmer Peak, scattered population along ridge top, in rocks and loose gravel in grassy area between shrubs, 16 Aug 1990, *J.C. Semple et al. 9339*, voucher for 2n = 18II (holotype: UC, Fig. 42; isotypes: CAN, CAS image, MO image, NY image, RSA!, WAT).

Heterotheca bolanderi has been recognized (e.g., Ferris, Munz, Jepson) as a distinct entity of west-central California characterized by its taprooted, caespitose habit, relatively large and generally few heads subtended by foliaceous capitular bracts that at least partly obscure the involucres. Leaves are greenish with sessile-glandular surfaces and relatively dense non-glandular vestiture (loosely strigose with long, fine hairs to strigose-villous or strigose-hirsute). Proximal cauline leaves are spatulate and petiolate, often withered by flowering; the distal are oblanceolate and epetiolate. Uppermost cauline leaves (peduncular bracts) and capitular bracts are as long or longer than the involucres.

Heterotheca bolanderi as most recently treated by Semple is viewed here as comprising three morpho-geographic elements: (1) the southernmost element is segregated as the previously undescribed species *H. sanctarum*; (2) the geographically central element, typical *H. bolanderi*, occurs from Santa Cruz, San Mateo, and Alameda counties into Sonoma Co.; and (3) the northern element, here recognized as *H. arenaria*, includes coastal strand/sandy-habitat populations from Marin Co. to Sonoma Co., Mendocino Co., and into southern Humboldt Co.

Semple (1992) found that inland populations of *Heterotheca bolanderi* are tetraploid, compared to the coastal diploids (here as *H. arenaria*). He observed that the diploid is restricted mostly to sandy, coastal strand habitats (sometimes on near-beach clay slopes and bluffs) while the tetraploid occurs on "mostly serpentine soils on hill and mountain tops surrounding San Francisco Bay" (Semple 1996). Tetraploid habitats are recorded as ridge tops, slopes, roadsides, in rocky and gravelly soil.

Although Semple noted in 1992 that most collections of var. *bolanderioides* had been previously identified as subsp. *bolanderi* (hence, presumably, the newly coined "-oides" epithet), the protologue diagnosis contrasted var. *bolanderioides* with [*H. sessiliflora*] var. *echioides*. Var. *bolanderioides* was distinguished in 1996 by a key couplet (p. 27) again contrasting it with var. *echioides*. Semple observed (1996, p. 49) that "individuals of var. *bolanderioides* can be similar in indument ..... to diploids of var. *echioides*, which usually has a leaf indument of dense spreading to appressed hairs obscuring the underlying glands and smaller involucres. It is uncertain whether var. *bolanderioides* is a tetraploid derivative of var. *echioides* or whether it may be an allopolyploid involving ssp. *echioides* and ssp. *bolanderi*." His hypothesis that var. *echioides* might be involved in the ancestry of var. *bolanderioides* apparently was based also on his observations (via keys and descriptions) that

the tetraploids (vs. diploids) range greater in height and ray ligule length and have a greater density of long hairs on the disc corolla lobes and tube.

In the present study it appears that Semple's concept of the *Heterotheca bolanderi* tetraploids included two elements: (1) a series of populations treated here as the separate species *Heterotheca sanctarum*, which is more similar to *H. echioides* (= *H. villosissima*) than to *H. bolanderi*, and (2) plants recognized as *H. bolanderi* sensu stricto.

The type of *Chrysopsis bolanderi* was collected from an inland area — the Berkeley Hills (including the "Oakland Hills" as noted by Bolander for the type collection, see Wikipedia entry for "Berkeley Hills"), with western slopes in Alameda County, eastern slopes in Contra Costa County — where apparently only the tetraploid occurs, and I find no morphological difference between the type of *C. bolanderi* and plants from the same area recorded by Semple as tetraploid. Semple (1996) mapped and cited only collections of var. *bolanderioides* and "aff. *bolanderioides*" from the Berkeley Hills of Alameda County as well as from Contra Costa County (including Vollmer Peak, the type locality of var. *bolanderioides*, in the Berkeley Hills) just outside Berkeley's eastern limit. His map shows diploids (*H. arenaria*) only along the immediate coastal strand.

Southernmost collections of typical *Heterotheca bolanderi*. Santa Cruz Co.: coastal terrace E of Calif Hwy 1 (Cabrillo Hwy) and across from Greyhound Rock parking lot, ca. 6 mi NW of Davenport, coastal prairie, 15 Aug 1982, *Buck 110* (JEPS) — *Buck 110* is typical in morphology but *Buck 111* (JEPS) from the same locality is unusual, with narrow leaves and heads lacking capitular bracts; San Vincente Rd, 3 mi from coastal hwy, ca. 500 ft, *Hesse 1379* (JEPS); San Vicente Rd, 2.5 mi from coast hwy, 475 ft, 26 Aug 1954, *Hesse 1380* (JEPS); Santa Cruz Terrace, coastal prairie, Swanton Pacific Ranch, 100-150 m, 13 Jul 2017, *Richardson 101* (OBI).

The only collection of typical *Heterotheca bolanderi* from Solano Co.: Mare Island, S end of island, 30 m, 18 Jun 2003, *Kelch & Murdoch AGM94* (JEPS).

Figure 39. *Heterotheca bolanderi*. Marin Co., Novato; photos by Jacob Martin, 17 Jun 2020. iNaturalist.

Figure 40. *Heterotheca bolanderi*. Marin Co., Mt. Tamalpais Watershed; photo by "kercado_eli," 14 Jun 2014. iNaturalist.

Figure 41. *Heterotheca bolanderi*. San Mateo Co., San Bruno Mountain Park; photo by Scott Loarie, 10 Jun 2012. iNaturalist.

Figure 42. *Heterotheca bolanderi*. Holotype (UC) of *H. sessiliflora* var. *bolanderioides*.

Figure 43. *Heterotheca bolanderi*, Marin County. *Eastwood 296* (US).

Figure 44. *Heterotheca bolanderi*, Marin County. *Rose 46270* (US).

Figure 45. *Heterotheca bolanderi*, Alameda County. *Ertter 14965* (BRY).

9. HETEROTHECA ARENARIA (Elmer) Nesom, **comb. nov.** *Chrysopsis arenaria* Elmer, Bot. Gaz. 41: 321. 1906. **TYPE**: **California**. Marin Co.: Point Reyes post office, [from the protologue: "dense prostrate mats on the windward side of the drifting sand dunes"], Jul 1903, *A.D.E. Elmer 4556* (holotype: A?; isotypes: CAS!, COLO image, DS!, GH image, NY-Fig. 50, RM, RSA!, US image).

The type of *Heterotheca arenaria* is from Marin County but the species becomes abundant in southern Mendocino County (around Anchor Bay) and northernmost Sonoma County, continuing northward to the apparent limit of its natural distribution in the Fort Bragg area (e.g., Noyo, Pudding Creek, 10-Mile River) and an extended record from Humboldt County. Disjunct plants in Washington state (cited below) apparently are adventive. During one part of this study, before realizing the major distinctions from typical *H. bolanderi*, I annotated collections of *H. arenaria* as "H. bolanderi var. mendocinoensis."

Heterotheca arenaria is distinct in its sandy habitats along the coastal strand. Label notes with *Jepson 17739* (JEPS), from near Fort Bragg, describe "Stems many, radiating from the root-crown and prostrate, with only ascending end, thus forming a densely close mat, quite thick and unbroken, an almost perfect circle 4 feet across." The spreading "stems" might be thought of as thin, elongate caudex branches or as scale-leaved rhizomes — Figures 46–52 show the rhizomes and colonial habit. Cauline leaves are densely clustered on the short stems, spatulate to obolong-oblanceolate or oblong-obovate, not clasping, the basal and proximal smaller and usually withered by flowering. Heads solitary on short branches, on distinct peduncles with reduced bracts; capitular bracts absent. Chromosome number, n=9 (Mendocino Co.: S of Westport, *Semple & Heard 8535* (MO!); Mendocino Co.: S of Mendocino, *Semple & Semple 5681* (BRIT!, MO!, NY-Fig. 51).

Vestiture of *Heterotheca arenaria* is similar to that of *H. bolanderi*, perhaps accounting for the two entities being treated as conspecific. Surfaces are sessile-glandular and loosely strigose to strigose-villous with long hairs; margins are ciliate with hairs quickly elongating into long, villous, filiform-flexuous distal portions.

Southernmost collections of *Heterotheca arenaria*: Sonoma Co.: Sea Ranch, near State Hwy 1, below S end of Yardarm Drive, Unit 15 Owners' Map, 16 Sep 1976, *Heknter 269* (UCD, not seen); Black Point Road, 13 Jul 1930, *Howell 5342* (CAS); 2 mi S of Anchor Cove, 2 Sep 1927, *Wolf 1345* (DS).

Northernmost collection of *Heterotheca arenaria*: Humboldt Co.: 2 mi S of Petrolia on Mattole River near where road crosses river, 30 Aug 1927, *Wolf s.n.* (SBBG 455062, as cited in Consortium of California Herbaria). Perhaps not part of the natural range.

Representative collections of *Heterotheca arenaria* from Washington state (adventive): Clallam Co.: E shore of Washington Harbor, steep sand bank above beach, 14 Sep 1921, *St. John 5869* (UC!, WS!) — annotated by Semple 1993 as "Probably adventive from Calif." Semple (1996) cited three other collections of *Heterotheca bolanderi* from Washington (all from Island Co.): *Gardner s.n.*, *Gardner 153*, and *Naas & Naas 5579*).

A collection identified here as *Heterotheca arenaria* is labeled as from Nevada Co., California, but is out of range and the label probably is in error: Nevada City, 19 Jul 1932, *McMinn 3025* (RSA).

Figure 46. *Heterotheca arenaria*. Top: Mendocino Co., Point Arena area; photo by 'avocat', 3 Aug 2019, iNaturalist. Bottom: Mendocino Co., north of Elk; photo by Asa Spade, 9 Aug 2019, iNaturalist.

Figure 47. *Heterotheca arenaria*. Mendocino Co., Mendocino Headlands State Park; photo by Karlyn H. Lewis, 7 Aug 2016, iNaturalist.

Figure 48. *Heterotheca arenaria*. Mendocino Co., MacKerricher State Marine Conservation Area; photo by Asa Spade 14 Aug 2019, iNaturalist.

Figure 49. *Heterotheca arenaria*. Mendocino Co., Point Arena-Stornetta Public Lands. Photos by Morgan Stickrod, 23 Nov 2020, iNaturalist.

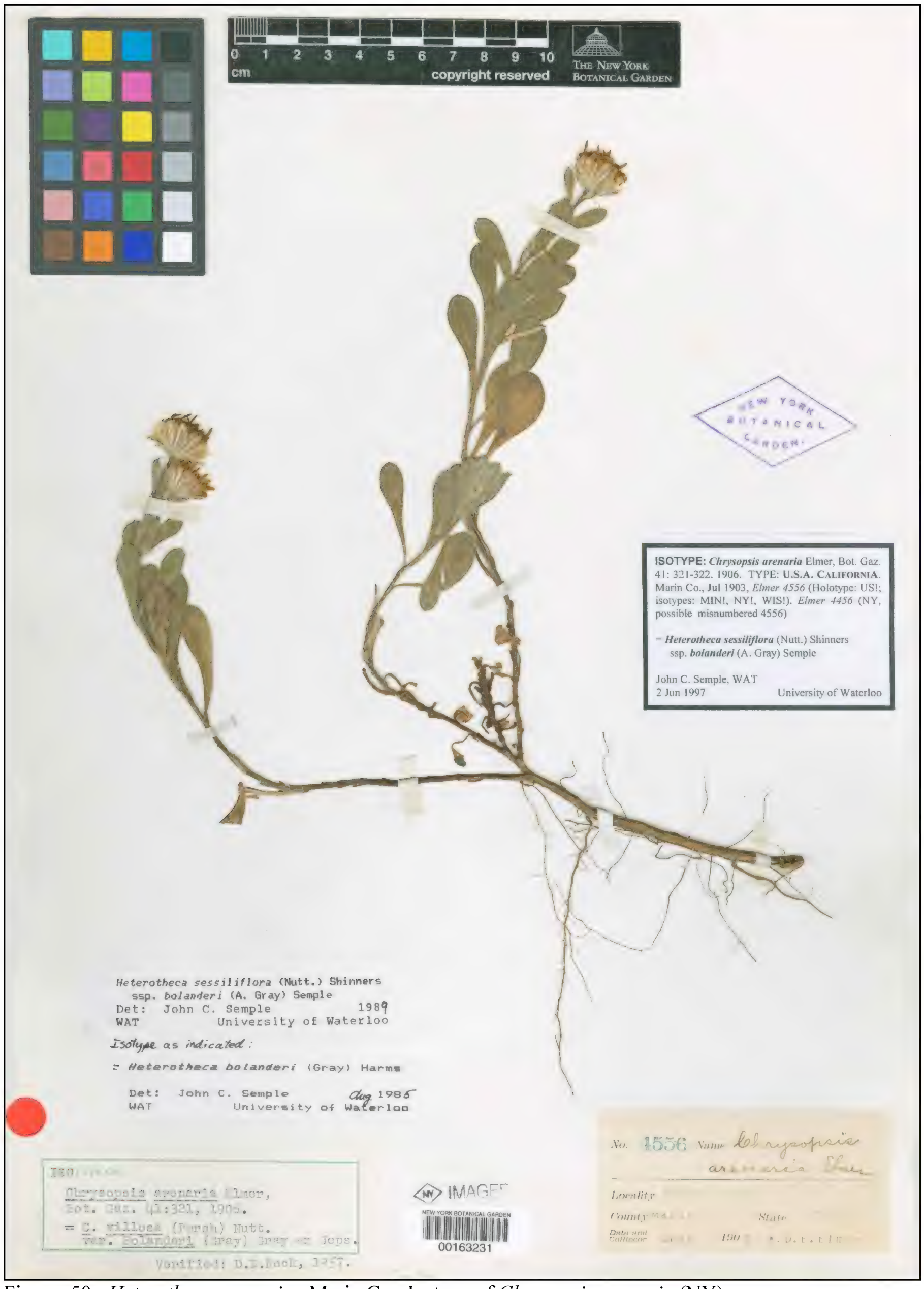


Figure. 50. *Heterotheca arenaria*. Marin Co. Isotype of *Chrysopsis arenaria* (NY).

Figure 51. *Heterotheca arenaria*. Mendocino Co., *Semple 5681* (NY). Voucher for diploid chromosome count of 2*n*=18. "Large population, plants forming low mats."

Figure 52. *Heterotheca arenaria.* Mendocino Co., *Howe 3581* (SDSU).

10. HETEROTHECA SANCTARUM Nesom, **sp. nov. TYPE**: **California**. Santa Clara Co.: Saratoga Summit (jct of Saratoga Road and Skyline Blvd), dry open hills, 750 m, 23 Sep 1941, *L.S. Rose 41459* (holotype: POM!; isotypes: BRU image, BRY!, CAS!, COLO image, DS!, GA image, LL!, MISSA image, MO-2 sheets!, PH-2 sheets!, RM!, SMU!, TEX-2!, UC!-Fig. 56, US-2 sheets images, Fig. 54). Semple (1996, p. 49) cited additional duplicates of *Rose 41459* at CAN, GH, NDG, NY, UBC, UNCC, and WIS.

Distinct in its densely overlapping, silvery-sericeous leaves without undulate margins, the basal and proximal early-withering, lack of axillary leaf clusters, heads in a closely corymboid cluster on short peduncles, capitular and subcapitular bracts mostly oblong to oblong-oblanceolate, 1/4–1/2 as long as the involucre and not at all obscuring it, bract margins densely long-ciliate. Different from *Heterotheca bolanderi* in its smaller, silvery-sericeous leaves and smaller capitular bracts. Different from *Heterotheca villosissima* in its villous stems, more densely overlapping leaves, and larger heads in a corymboid cluster (shorter peduncles). See key couplets below.

Perennials, apparently from woody rhizome or rhizome-like caudex branches (*Fosberg 43225*: "small clumps, erect, usually of a few stems"). **Stems** strictly erect, 20–40 cm tall, stems vestiture 1-storied, sparsely villous with long, irregularly spreading hairs, minutely and inconspicuously glandular, especially distally. **Leaves**: basal and lower cauline (proximal half of stem) withered and shed by flowering, persistent cauline usually densely overlapping, ascending, sessile, often subclasping, mostly oblong-oblanceolate to oblong-lanceolate, 10–25(–40) x 2–8 mm, densely but loosely silvery sericeous to silvery gray on both surfaces, surfaces minutely and obscurely glandular, mostly obscured by the non-glandular vestiture of fine, thin-based hairs, base truncate, apex rounded-apiculate to acute-apiculate, margins not undulate; axillary clusters of small leaves usually absent. **Heads** in a loose to closely corymboid arrangement, peduncles relatively short (mostly 10–25 mm), longer on proximal branches. **Involucres** 12–17 mm wide (pressed), inner phyllaries 6–9 mm long, oblong-lanceolate to linear-lanceolate; phyllaries sparsely to moderately strigose-sericeous, minutely glandular; capitular and subcapitular bracts mostly oblong to oblong-oblanceolate, 1/4–1/2 as long as the involucre, not at all obscuring the involucre, bract margins densely long-ciliate. **Ray florets** 10–15.

Flowering (May-)Aug-Oct; sandstone, rocky slopes, grassland, chaparral openings, blue oak woodland, 500–2800(–3800) ft.

Tetraploid counts of *Heterotheca sanctarum* have been made from Santa Clara and Santa Cruz counties (*Semple 5670*, *Semple & Chmielewski 8915*, *8916* [$2n$ =18II and 14II + 2IV], *8918*, *8924* [diploids, triploids, tetraploids present, fide Semple 2008] and *8926*). A count by Semple (fide label data, *Semple & Chmielewski 8919*) suggests that diploids occur in Santa Cruz Co. but this collection is a mix of *H. sanctarum* and H. *camphorata* (identified in Semple 2008 as "aff. var. *echioides*") and the diploid count needs to be verified, since all counts of *H. camphorata* have been diploid. It seems likely that *H. sanctarum* is consistently tetraploid.

Heterotheca sanctarum is sympatric with *H. camphorata* in Santa Clara, Santa Cruz, and San Benito counties and hybrids apparently are formed in Santa Clara Co., although the two species remain distinct for the most part. Possible evidence of gene flow shows in glandular involucres of *H. sanctarum* otherwise of characteristic morphology.

Heterotheca sanctarum, for the most part, was identified by Semple (by citation in 1996 and by annotation) within his concept of *H. bolanderi* var. *bolanderioides*. Plants of *H. sanctarum*, however, are distinct from both varieties of *H. bolanderi* in their silvery-sericeous leaf vestiture, which often more resembles that of *H. villosissima* and *H. fastigiata*. Treatment of *H. sanctarum* at specific rank allows that this entity may be as closely related (or more closely) to *H. villosissima* as to *H. bolanderi*. This similarity may underlie Semple's diagnostic comparison of his var. *bolanderioides* [emphasizing the *H. sanctarum* populations] to var. *echioides* (= *H. villosissima*).

1a. Leaves silvery to silvery-gray, 10–25(–40) x 2–8 mm; heads with capitular bracts 1/4–1/2 as long as the involucre, not at all obscuring the involucre ..... **Heterotheca sanctarum**

1a. Leaves gray-green, mostly 20–45(–55) x 3–10 mm; heads (in var. *bolanderi*) with capitular bracts mostly as long or longer than the involucre, obscuring the involucre ..... **Heterotheca bolanderi**

1b. Capitular bract margins densely long-ciliate; involucres 12–17 mm wide (pressed); axillary clusters of small leaves mostly absent; stems villous; inflorescence characteristically corymboid; tetraploid ..... **Heterotheca sanctarum**

1b. Capitular bract margins ciliate but not prominently long-ciliate; involucres (8–)10–14 mm wide (pressed); axillary clusters of small leaves consistently present; stems hirsute; inflorescence characteristically subcorymboid to elongate-paniculate; diploid ..... **Heterotheca villosissima**

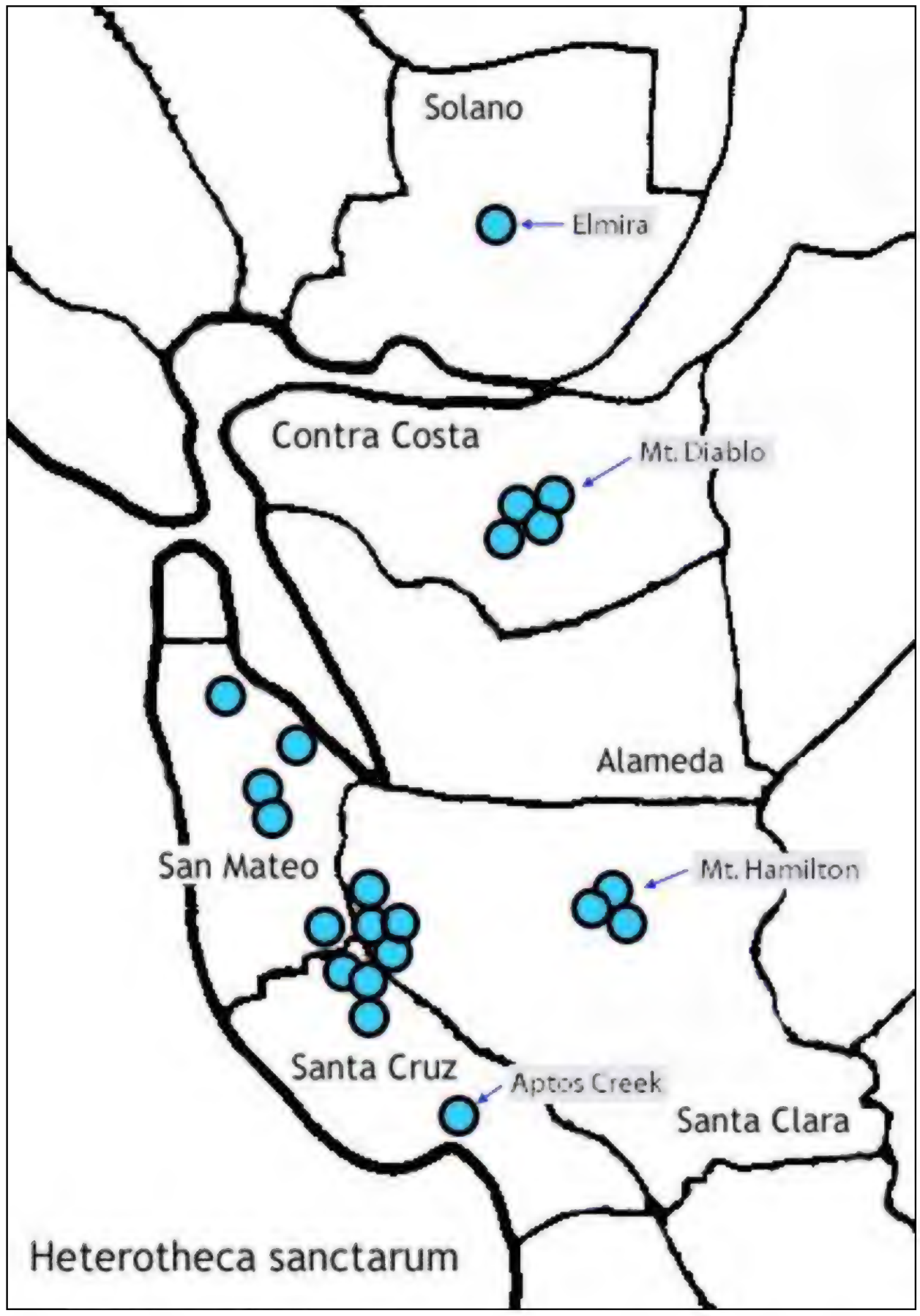


Figure 53. Distribution of *Heterotheca sanctarum*. Outlying localities are in Solano Co. (Elmira), Contra Costa Co. (Mt. Diablo), Santa Clara Co. (Mt. Hamilton), and Santa Cruz Co. (Aptos Creek). See Map 3 for broader context.

Additional collections examined. **California**. Contra Costa Co.: Mt. Diablo, Mt. Zion near base, open grassy hillside, 2 Dec 1930, *Bowerman 501* (UC); Black Diamond Mines Regional Preserve S of Pittsburgh, steep S-facing side of Rose Hill above cemetery near sandstone outcrops, ca. 1200 ft, 5 May 1991, *Ertter 9770* (UC); S side of Mt. Diablo, W end of Black Hawk Ridge, above chaparral on S slope, 2000 ft, 2 Sep 1996, *Ertter 15275* (BRIT, UC); SW side of Mt. Diablo, Wall Point Rd across Pine Ridge ca. 1/2 air mi ENE of Macedo Ranch, blue oak woodland on sandstone, 24 Nov 1996, *Ertter 15415* (UC); W flank of Mt. Diablo, Shell Ridge Open Space, exposed sandstone on main ridgeline, 16 Feb 1997, *Ertter 15458* (UC); SW side of Mt. Diablo, Secret Trail at head of Pine Canyon, oak woodland on sandstone, 14 Sep 1997, *Ertter 15812* (UC); Mt. Diablo, dry hillside, 5 Oct 1933, *Schreiber 940* (UC); Mt. Diablo State Park, Wall Point, grassland, 1450 ft, 29 Jun 2015, *Slakey 134* (UC). San Mateo Co.: ridge between Slate and Oil Creek, 2200 ft, 21 Jun 1935, *Carlson 77* (UC); Corte de Madera, 23 Sep 1906, *McGregor s.n.* (CAS); San Bruno Mtn., open slopes, ca. 1200 ft, 20 Aug 1966, *Rose 66087* (BRY, OBI, UC); Coal Mine Ridge, near Stanford University, 22 Sep 1906, *Rust 6* (DS). Santa Clara Co.: Saratoga, dry exposed slopes, 6 Oct 1906, *Abrams s.n.* [x *H. camphorata*?] (CAS, UC, WTU); Castle Rock Ridge, 7 Oct 1906, *Abrams s.n.* (DS); Black Mtn, occasional on open, grassy slopes, 20 Oct 1901, *Baker 56* (MO, POM); Black Mtn on Palo Alto Rd, *Baker 2418* (LL); Page Mill Rd, E slope of Santa Cruz Mts, dry bank, ca. 500 ft, 24 Jun 1934, *Blake 11759* (LL); W slope of Mt. Hamilton, dry gravelly slope, blue oak, 3800 ft, Sep 1934, *Ewan 8939* (UC); 8 mi from San Jose on road to Mt. Hamilton, 13 Aug 1933, Howell 11511 [x *H. camphorata*?] (CAS); Castle Rock Ridge, 3 mi S of jct of Skyline Blvd and Saratoga Rd, dry open slopes, 2200 ft, 21 Sep 1937, *Rose 37666* (CAS, PH, RSA, UC); Page Mill Rd, NE of Calif Hwy 35, serpentine roadside, 85 road embankment, 21 Sep 1987, *Semple & Chmielewski 8915* (MO, RSA); Palo Alto on Page Mill Rd, 9.0 km NE of Calif Hwy 35, Foothills Park area, roadside embankment, 21 Sep 1987, *Semple & Chmielewski 8916* (MO); W of Palo Alto on Calif Hwy 35, 17.5 km SE of Hwy 84, Santa Clara MilePost 17.5, 22 Sep 1987, *Semple & Chmielewski 8918* (RSA-the 2 stems on left, larger stem on right is *H. camphorata*); Mt. Hamilton Rd to Lick Observatory, ca. milepost 18.53 at sharp corner in road, open roadside embankment, 23 Sep 1987, *Semple & Chmielewski 8924* (MO); Mt. Hamilton Rd to Lick Observatory, ca. milepost 14.62 at sharp corner in road, exposed rock, 23 Sep 1987, *Semple & Chmielewski 8926* (MO); W slope of Mt. Hamilton dry rocky exposed slopes, 2750 ft, 1 Sep 1934, *Sharsmith 1354* (TEX, UC); W slope of Mt. Hamilton, 1/2 mi by road above Hall's Valley, dry rocky exposed slopes on upper slopes of mountain, 2150 ft, 21 Oct 1934, *Sharsmith 1411* (UC); W side of Mt. Hamilton near summit, grassy slope in *Pinus sabiniana* belt, 4300 ft, 13 Sep 1936, *Sharsmith 3889* (UC); Mt. Hamilton, Sep 1904, *Smith s.n.* (UC); Mt. Hamilton foothills, 9 Sep 1908, *Smith s.n.* [x *H. camphorata*?] (JEPS); Monte Bello Ridge, ca. 8.5 mi S from Palo Alto, between summit of Black Mtn and Page Mill Rd, open grassland, ca. 2400 ft, 3 Oct 1965, *Thomas 11454* (RSA). Santa Cruz Co.: head of Aptos Creek, 12 Oct 1902, *Abrams 3073* (RM); 4 mi SE of Saratoga Gap on Summit Rd, Santa Cruz Mts, common in chaparral opening, 900 m, 3 Sep 1962, *Fosberg 43225* (POM); near Saratoga summit, ca. 2500 ft, 2 Sep 1954, *Hesse 1211* (UC), *1388* (UC), *1389* (UC); 7 mi WSW of Saratoga, 2000 ft, 29 Apr 1935 [old stems], *Johannsen 605* (UC); Castle Rock Ridge, 3 mi S of the jct of Skyline Blvd. and Saratoga Rd, 670 m, 21 Sep 1937, *Rose 37666* (UC); Calif Hwy 35 NW of Saratoga, high elevation, 20 Aug 1981, *Semple 5670* (JEPS, MO); Calif Hwy 35, 5.6 km S of Calif Hwy 9, near rock exposure along roadside, 22 Sep 1987, *Semple & Chmielewski 8919* (MO); ca. 1 mi S of Saratoga Summit, 3 Oct 1953, *Thomas 3590* (CAS, RSA); Castle Rock Ridge, 2500 ft, 29 Jul 1934, *Yates s.n.* (RM). Solano Co.: Fields near Elmira, 11 Jun 1910, *Toy s.n.* (DS).

Figure 54. *Heterotheca sanctarum*, Santa Clara Co. Isotype (US).

Figure 55. *Heterotheca sanctarum*. Detail from US isotype shown in Figure 54.

Figure 56. *Heterotheca sanctarum*, Santa Clara Co. Isotype (UC).

Figure 57. *Heterotheca sanctarum*, Santa Cruz Co. *Yates 4954* (UC).

Nesom: *Heterotheca* sect. *Phyllotheca*

Figure 58. *Heterotheca sanctarum*, Santa Cruz Co. *Hesse 1211* (UC).

Figure 59. *Heterotheca sanctarum*. San Mateo Co., Russian Ridge Open Space Preserve. Photo by Will Ferguson, 18 Nov 2018. iNaturalist.

Figure 60. *Heterotheca sanctarum*. Detail from Figure 58.

Figure 61. *Heterotheca sanctarum*. Santa Clara Co., Sierra Azul Open Space. Photo by Edward Rooks, 5 Oct 2018. iNaturalist.

Nesom, G.L. 2020. A new species of *Ionactis* (Asteraceae: Astereae) from the east Gulf Coastal Plain. Phytoneuron 2020-91: 1–24. Published 18 December 2020. ISSN 2153 733X

A NEW SPECIES OF *IONACTIS* (ASTERACEAE: ASTEREAE) FROM THE EAST GULF COASTAL PLAIN

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ABSTRACT

A population system of *Ionactis* from the east Gulf Coastal Plain is recognized as **Ionactis repens** Nesom, **sp. nov.**, discontinously distinct in morphology and geography from the widespread *I. linariifolia*. The new species differs in its creeping, scale-leaved rhizomes and evidently colonial habit and in its reduced branching that produces solitary heads on long, bracteate, peduncle-like branches. Maps and illustrations of both species are provided.

Recent taxonomic revisions of *Ionactis* Greene (Nesom & Leary 1992; Nesom 2006) have recognized five species — one widely distributed in the eastern USA and southeastern Canada (*I. linariifolia* (L.) Greene) and four of limited distributions in the western USA.

The large-scale distribution of *Ionactis linariifolia* is patchy (Fig. 2), especially west of the Mississippi River, and regional differentiation might be expected. In a review made possible by online specimen images, variation in *I. linariifolia* is evident in branching pattern, leaf size, head size, and ray color — some of this is roughly correlated with geography but consistent patterns are not evident. Plants of a population system along the southern margin of the east Gulf Coastal Plain (Fig. 1), however, are discontinuously distinct from the rest of the species, differing most conspicuously in habit and position and abundance of branching. This system is formally recognized here as a distinct species.

IONACTIS REPENS Nesom, **sp. nov.** **TYPE**: **Alabama**. Washington Co.: Vicinity of Leroy on US Hwy 43, ca. 1 mi S of Leroy jct, cutover longleaf pine hills, 22 Oct 1969, *R. Kral 38273* (holotype: BRIT, Fig. 3; isotypes: FSU image, GA image, TENN image).

Similar to the widespread *Ionactis linariifolia* but distinct in its combination of branching, creeping, scale-leaved rhizomes and evidently colonial habit (vs. caespitose habit, without rhizomes, stems arising from a compact, woody, fibrous-rooted crown), solitary heads on long, bracteate peduncle-like branches arising from midstem or slightly above (vs. heads relatively crowded from shorter, distal branches), and its distribution on the east Gulf Coastal Plain.

Plants with branching, creeping, scale-leaved rhizomes, apparently at least weakly colonial. **Stems** erect to ascending-erect, 10–40 cm long, unbranched or few-branched above the middle. **Leaves** uniform, glabrous, linear to narrowly oblong or oblanceolate, midstem 9–22 mm long, 0.8–1.5 mm wide, faces glabrous, eglandular. **Heads** solitary on long, bracteate peduncle-like branches arising from midstem or slightly above. **Involucres** 7–9 mm wide (pressed), phllaries in (4–)5–6 series strongly graduate in length, apices obtuse to rounded. **Ray flowers** 8–12, corollas blue. **Chromosome number**, $2n = 18$ [Florida. Franklin Co.: S of Sumatra, open pine woods, 24 Oct 1999, *Semple 10930*, USF image]. Figures 3-11.

Flowering October-November. Hills, flats, clearcuts, sand, red clay, silty clay, sandy peat, longleaf pine, longleaf pine-wiregrass savannas, longleaf pine-scrub oak, pine-galberry flatwoods, live oak-pine, loblolly-longleaf pine; 20–370 ft.

Taxonomic rank of eastern USA *Ionactis*

Because of the similarity of the rhizomatous and non-rhizomatous plants and their clear sister evolutionary relationship, recognition at varietal rank might be preferred by some, keeping all of eastern USA *Ionactis* as a single species. The choice here emphasizes the apparent discontinuity in morphology and geography, central in most species concepts. The degree of morphological difference between these two entities is small in the context of their overall similarity and larger morphological gaps between *Ionactis* species of the western USA, but reliance on degree of difference is subjective.

Geography provides confidence in the distinction of *Ionactis repens*, as its range corresponds almost exactly with phytogeographic pattern #10 of Sorrie and Weakley (2001) — the "East Gulf Coastal Plain," which characterizes the distribution of many other endemic species. The EGCP was "an important refuge for plants during Pleistocene glaciation cycles" (Sorrie & Weakley, p. 59). The outlier of *I. repens* in Nassau Co., Florida (*Beckner s.n.*, FLAS-Fig. 10), appears to be disjunct, as the intervening area has been well collected. The occurrence of *I. linariifolia* sensu stricto in St. Helena Par., Louisiana (*Allen 189*, LSU; *Smith s.n.*, LSU; *Stam 117*, LSU) where *I. repens* would be expected, seems unusual.

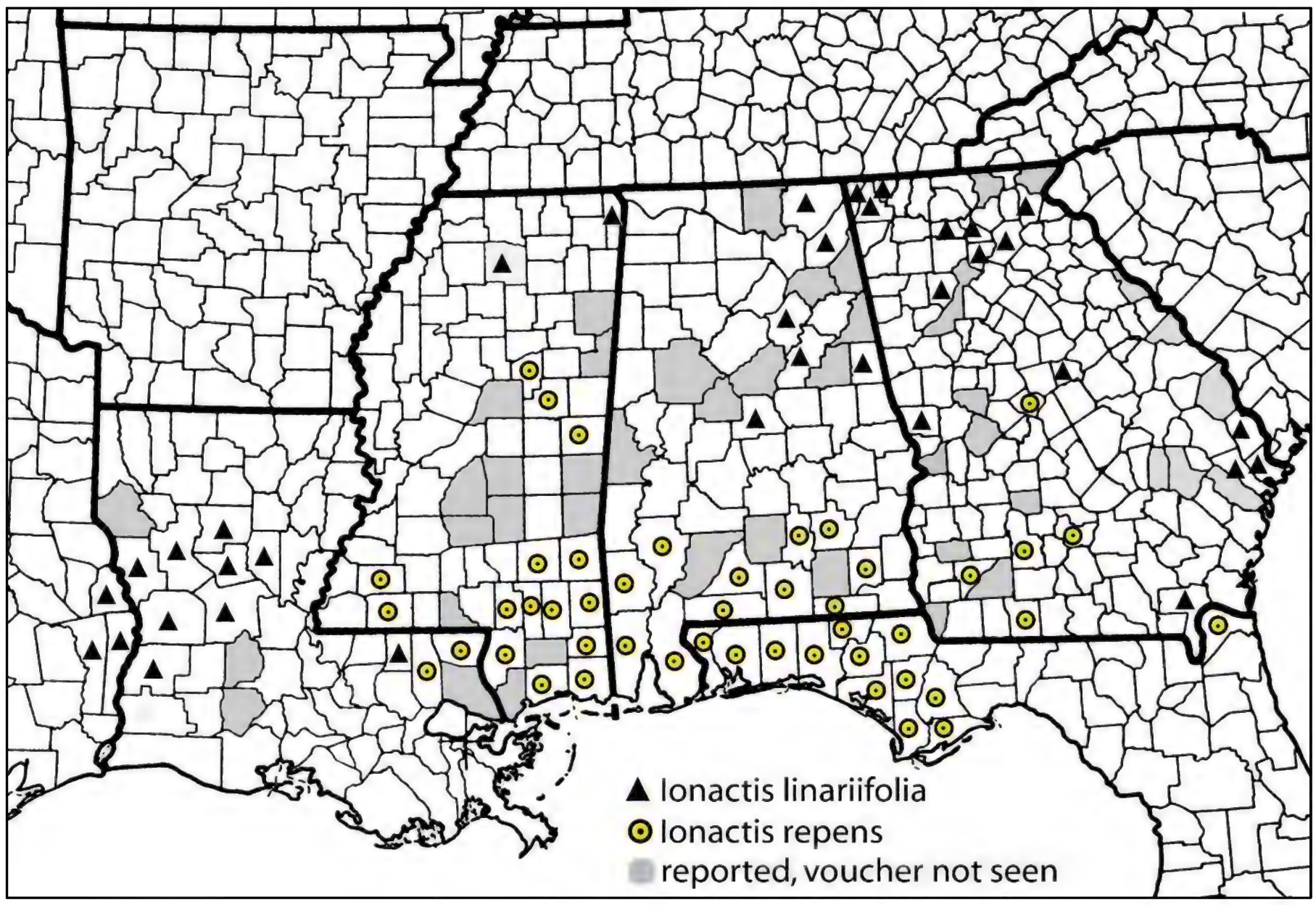

Figure 1. Distribution of *Ionactis repens* and *I. linariifolia* in the east Gulf Coastal Plain. Gray-shaded counties are those where *Ionactis* has been reported but for which a voucher has not been seen in this study. Possible sympatry of the two species remains to be determined.

Alan Weakley and Derick Poindexter (UNC Chapel Hill; pers. comm.) have pointed out that non-rhizomatous plants similar to *Ionactis repens* in branching pattern and very narrow leaves occur in a small area of the North Carolina-South Carolina coastal plain. These possibly represent a third entity of the genus in the eastern USA.

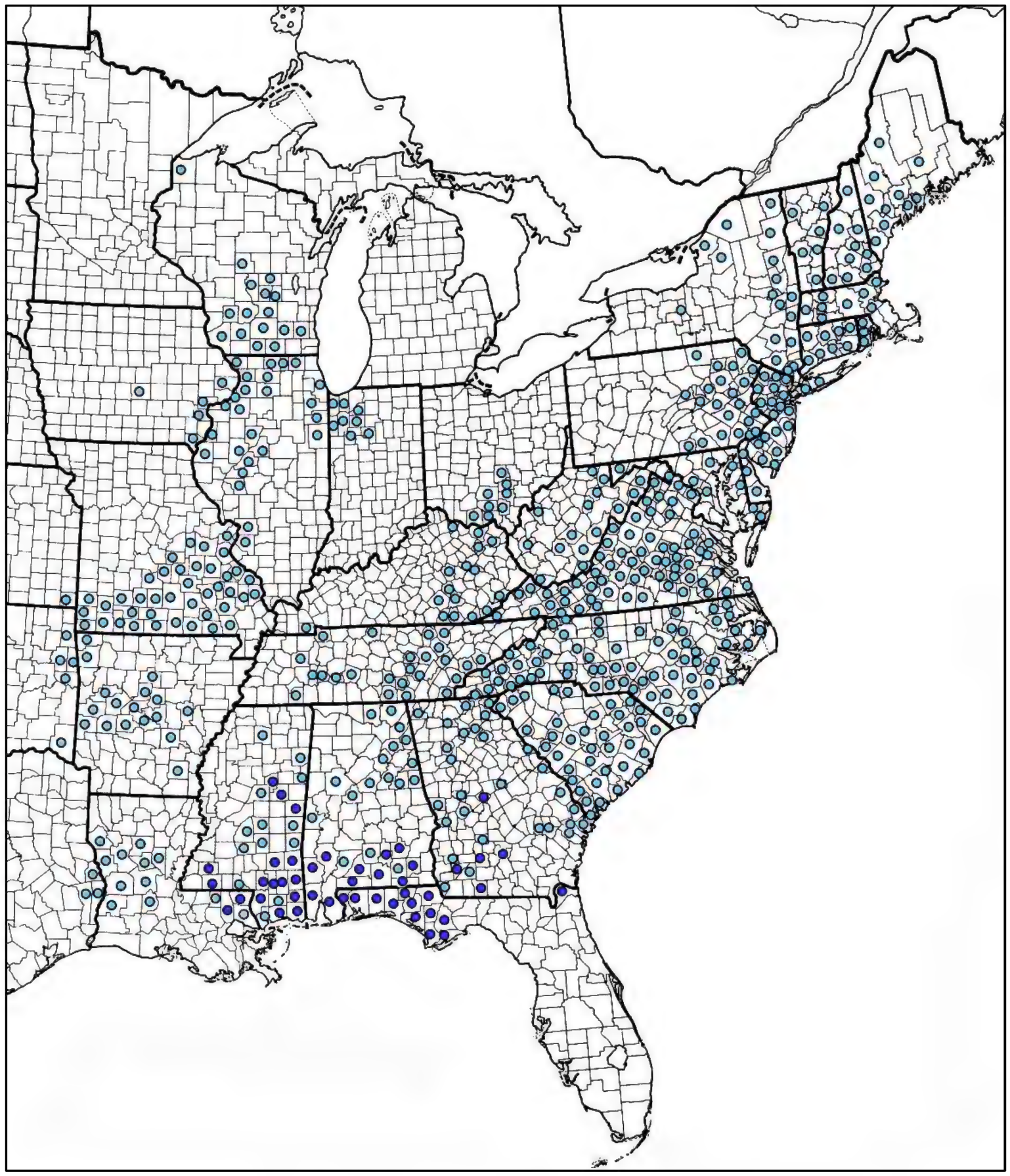

Figure 2. Distribution of *Ionactis* in the eastern USA. Records from various sources. Dark blue symbols are records of *I. repens* for which vouchers have been seen (cf. Figure 1).

Ancestral character states of the eastern USA species

Between *Ionactis repens* and *I. linariifolia*, which branching pattern and which habit is the more primitive is speculative. Each of the four western species produces solitary (or few) heads and none of them produces long, scale-leaved rhizomes — *I. alpina* and *I. stenomeres* (Figs. 21 and 22) are closest in overall appearance to the eastern species. Thus, the relatively greater abundance of axillary buds and branching in typical *I. linariifolia* might be interpreted as a derived feature. Similarly, the long rhizomes of *I. repens* may be derived. There is no evidence to suggest that one of the eastern species is derived from the other.

The rhizomes characteristic of *Ionactis repens* perhaps are an adaptation to habitats of loose sand, where the species usually occurs. On the other hand, typical *I. linariifolia* occurs in a wider range of habitats but also occurs in sandy habitats (e.g., in Louisiana and Texas, the Atlantic coastal plain). At least the rhizomatous habit of *I. repens* does not appear to be merely a phenotypic response.

Figure 3. *Ionactis repens*. Washington Co., Alabama, *Kral 38273*. Holotype (BRIT).

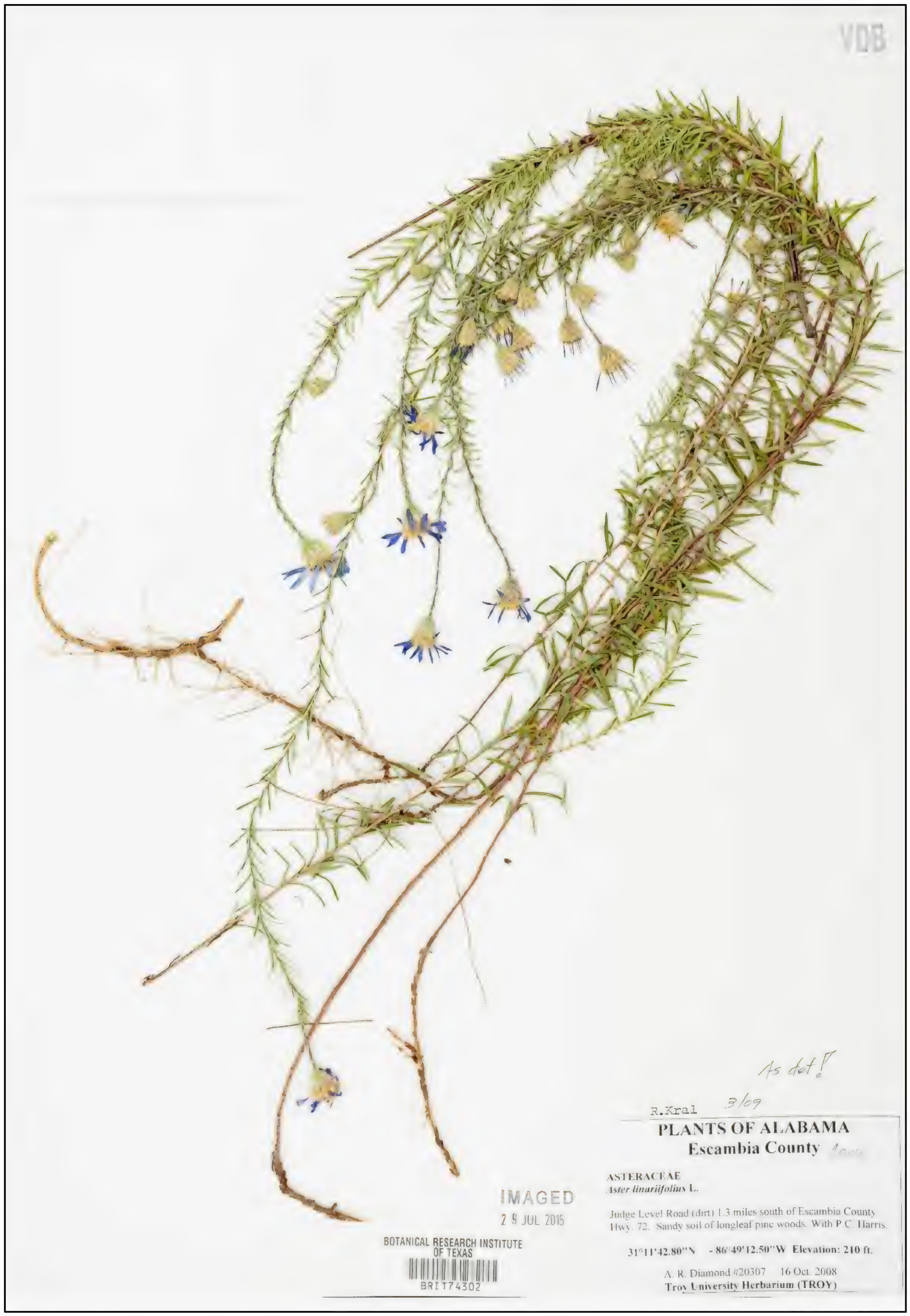

Figure 4. *Ionactis repens*. Escambia Co., Alabama, *Diamond 20307* (BRIT).

Figure 5. *Ionactis repens*. Conecuh Co., Alabama, *Diamond 8943* (AUA).

Nesom: *Ionactis repens*, sp. nov.

Figure 6. *Ionactis repens*. Covington Co., Alabama, *Kral 38135* (BRIT).

Figure 7. *Ionactis repens*. Baker Co., Georgia, *Thorne 7312* (GEO).

Figure 8. *Ionactis repens*. Gulf Co., Florida, *Gholson 3606* (BRIT).

Figure 9. *Ionactis repens*. Calhoun Co., Florida, *Orzell & Bridges 38273* (USF).

Figure 10. *Ionactis repens*. Nassau Co., Florida, *Beckner s.n.* (FLAS).

Figure 11. *Ionactis repens*. Base of plants from collections shown in Figs. 3-10. Arrows point to rhizomes.

Figure 12. *Ionactis linariifolia*. Dekalb Co., Alabama, *McDaniel 22974* (GA).

Figure 13. *Ionactis linariifolia*. Dawson Co., Georgia, *Cronquist 4784* (GEO).

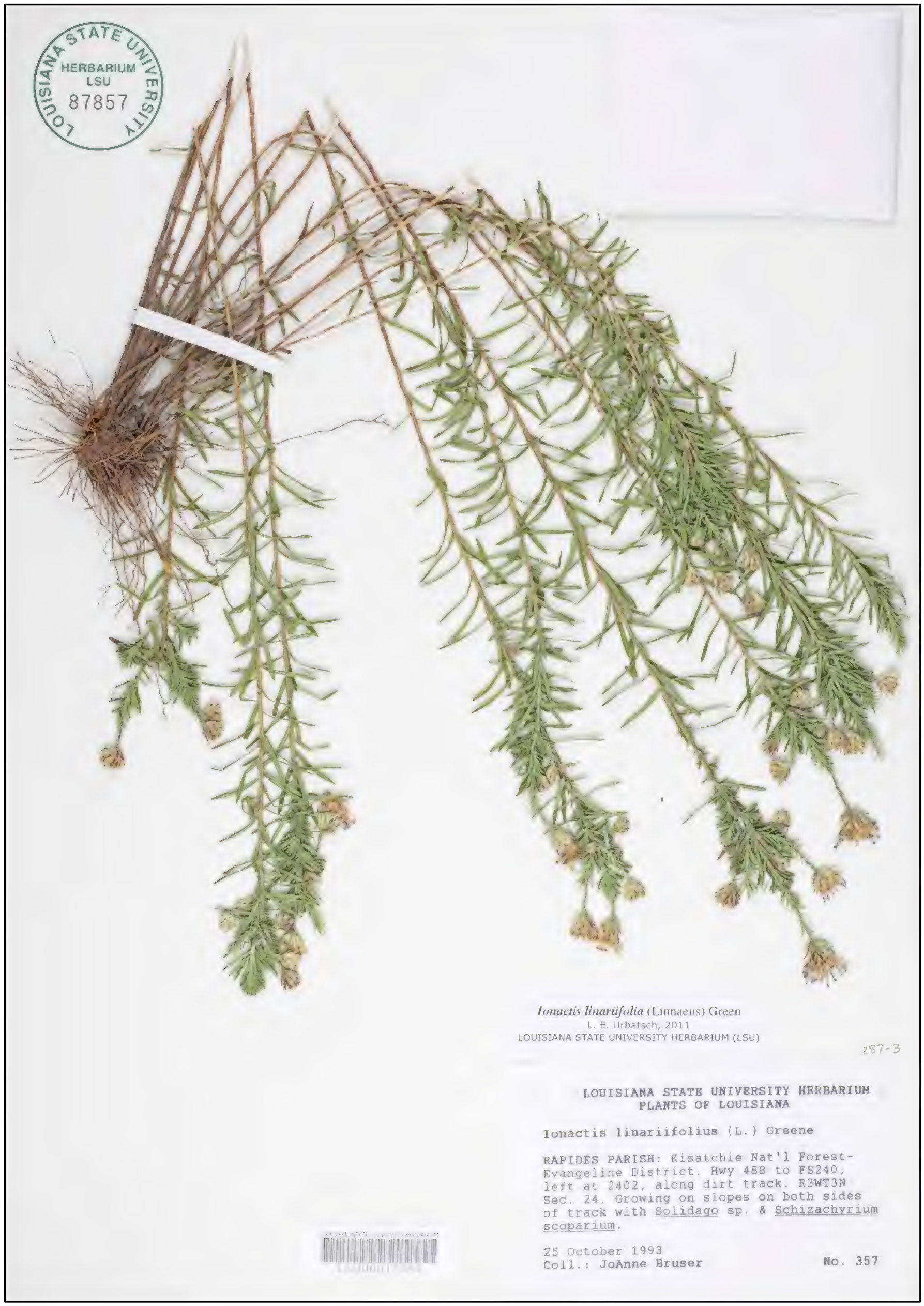

Figure 14. *Ionactis linariifolia*. Rapides Par., Louisiana, *Bruser 357* (LSU).

Figure 15. *Ionactis linariifolia*. Jasper Co., Texas, *Orzell & Bridges 8725* (TEX).

Figure 16. *Ionactis linariifolia*. Saline Co., Arkansas, *Witsell 03-1012* (ANHC).

Figure 17. *Ionactis linariifolia*. Jefferson Co., Missouri, *Raven 27625* (KANU).

Figure 18. *Ionactis linariifolia*. Chesterfield Co., South Carolina, *Daggy 5861* (UNCC).

Figure 19. *Ionactis linariifolia*. Arlington Co., Virginia, *Blake s.n.* (COLO).

Figure 20. *Ionactis linariifolia*. Luzerne Co., Pennsylvania, *Witte s.n.* (CHRB).

Figure 21. *Ionactis alpina*. Box Elder Co., Utah, *Neese 11621* (BRY).

Figure 22. *Ionactis stenomeres*. Silver Bow Co., Montana, *Lackschewitz 9738* (COLO).

ACKNOWLEDGEMENTS

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Nesom, G.L. 2020. Bigelowia *nudata* (Asteraceae): Subspecies at specific rank. Phytoneuron 2020-92: 1–32. Published 18 December 2020. ISSN 2153 733X

BIGELOWIA NUDATA (ASTERACEAE): SUBSPECIES AT SPECIFIC RANK

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ABSTRACT

Bigelowia nudata subsp. *australis*, a Florida endemic, is recognized here at specific rank as **Bigelowia australis** (L.C. Anderson) Nesom, **comb. et stat. nov.**, morphologically and geographically distinct from typical and more widespread *B. nudata*. Gene flow may occur where the two are sympatric in northwestern Florida but a marked distinction in growth habit appears to be constant. In situ photos, images of herbarium specimens, and a distribution map are provided.

Bigelowia DC. comprises two species, following Anderson (1970, 1972, 1977) — *B. nudata* (Michx.) DC., with two subspecies, and *B. nuttallii* L.C. Anderson. Although the morphological distinction between the subspecies of *B. nudata* might appear to be quantitative and subtle, Anderson found a sharp geographical divide. Subsp. *nudata* (Figs. 2-8) occurs in northern Florida to eastern Louisiana and to North Carolina, while subsp. *australis* L.C. Anderson (Figs. 9-18) is confined to peninsular Florida. Anderson's interpretation has been accepted by Nesom (2006) and Weakley (2020), but a review here based on specimen images (SERNEC, herbarium US) and in situ photos (iNaturalist) provides a different interpretation.

The two *Bigelowia nudata* entities have essentially contiguous ranges as identified and mapped by Anderson (1970), but he noted the occurrence of scattered intermediates in northeastern Florida within his mapped range of typical *B. nudata*. The putative intermediates were the basis for Anderson's choice of taxonomic rank (Anderson 1977, p. 214): "Sufficient intermediates have been found to warrant the taxonomic recognition as subspecies." A rationale for assignment of rank was not given in 1970, but was likely based on the newly popular (in botany) use of subspecies as the infraspecific a rank of choice when there was some indication of imperfect separation of two taxonomic entities, as by the existence of some “intermediate” specimens. Use of varietal rank by Shinners (1971) was simply to provide taxonomic "uniformity" in a project in which he was using variety as the infraspecific rank of choice, according with traditional usage in botany and with the much more general availability at the time of infraspecific combinations at that rank.

The contrasting interpretation here is that consistent, distinct geographies and morphologies (especially a biologically significant feature of growth habit) justify recognition of each of the two entities at specific rank, and I identify Anderson's putative intermediates as *Bigelowia australis* occurring in sympatry with *B. nudata* (Fig. 1). Typical *B. australis* occurs in the area of sympatry (as documented below by specimen citations) although morphology ambiguously suggests that some collections identified here as *B. australis* may show evidence of genetic interchange with *B. nudata*. In the area of sympatry, both entities flower in late August through October, allowing the possibility of hybridization, although there is a degree of ecological isolation, with *B. australis* tending to grow in wetter habitats. The area of sympatry does not appear to be one of intergradation — additional observations are necessary toward a better understanding of the biological interaction between the two entities.

1. Plants commonly occurring in close clusters; proximal leaves with a distinctly narrowed petiolar region, blade elliptic to oblanceolate, mostly 4–14 mm wide, crowded in a basal rosette (the leaves mainly appressed to the ground or somewhat ascending); involucres 4–6 mm high; florets 2–5, corollas 3–4 mm long ..... **Bigelowia nudata**

1. Plants occurring singly; proximal leaves usually without a clearly distinct petiolar region, linear to linear-oblanceolate, mostly 2–4 mm wide, usually relatively few and not forming a prominent rosette (the basal and lower stem leaves held vertical to the stem or strongly ascending); involucres 6–7.5 mm high; florets 3–6, corollas 4–5 mm long ..... **Bigelowia australis**

BIGELOWIA NUDATA (Michx.) DC., Prodr. 5: 329: 1836. *Chrysocoma nudata* Michx., Fl. Bor. Amer. 2: 101. 1803. *Aster nudatus* (Michx.) Kuntze, Rev. Gen. 1: 318. 1891. *Chondrophora nudata* (Michx.) Britton, Mem. Torrey Bot. Club 5: 317. 1894. Protologue. "In humidis Carolinae." **TYPE**: "Ameriq, Sept," *A. Michaux* (probable holotype: P 703201 image; probable isotype: 703202 image).

Pine flatwoods, sandy prairies, hillside seepage bogs, moist sandy roadbanks; flowering August–October.

BIGELOWIA AUSTRALIS (L.C. Anderson) Nesom, **comb. et stat. nov.** *Bigelowia nudata* subsp. *australis* L.C. Anderson, Sida 3: 463. 1970. *Bigelowia nudata* var. *australis* (L.C. Anderson) Shinners, Sida 4: 274. 1971. **TYPE**: **Florida**. Lee Co.: Vicinity of Ft. Myers, in pineland, 20 Mar 1916, *J.P. Standley 28* (holotype: NY; isotypes: GH image, MO image, US image).

Wet sandy prairies, wet ditches, wet loam of palmetto stands, cypress swamps, pine flatwoods; flowering (August–)September–November(–May). Anderon (1970) noted that the range of *Bigelowia australis* is "rapidly being reduced by 'advances of civilization' (Lakela, personal communication)."

Anderson (1970, p. 452) characterized plants of typical *Bigelowia nudata* as "cespitose with a short, stocky caudex … Occasionally, layering by sediments results in an elongated, rhizome-like caudex." For *B. australis*, he noted that "caudices are elongate, only moderately thickened, and frequently connected by short rhizomes." Observations here generally confirm Anderson's characterization of their similarity (but not his explanation of origin of rhizomes in *B. nudata*). A difference in growth habit, however, appears to be the most consistent and unambiguous feature distinguishing them — in fact, it may be that identifications by collectors have relied, implicitly, on growth habit as much or more than the quantitative, overlapping size differences for involucres and leaves usually given in keys.

Plants of *Bigelowia australis* occur singly, with proximal leaves narrow, erect-ascending to erect, and usually not congested in a basal rosette — the rhizomes apparently do not lead to colonial growth (Figs. 23-25, Fig. 27). Collections of *B. nudata* often show only a cluster of fibrous roots, but others show short, thickened rhizomes similar to those of *B. australis*. (Fig. 28). Plants of *B. nudata*, however, tend to occur in close clusters, suggesting a colonial habit, with proximal leaves broader, spreading, and in a distinct basal rosette (Figs. 19-22).

A collection of otherwise typical *Bigelowia nudata* from Calhoun Co., Florida (Fig. 29), shows the production of elongate, filiform rhizomes with plantlets at the tips. This is the only collection over the whole geographic range that I have seen with this feature, but this is what might be expected to produce the characteristic, colonial clusters of plants. This suggests to me (speculatively, admittedly) that these slender rhizomes may be ephemeral and usually produced mostly during times when collectors are not making specimens. Alternatively, it may be that some of what appear to be thickened fibrous roots may actually be rhizomes (not apparent from the digital images) and that fragile inter-plant connections are not observed or preserved by most collectors. Or, perhaps this population is genetically unique within the species.

Anderson (1970, p. 464) noted that the morphology of *Bigelowia australis* "is intermediate to that of [*B. nudata*] and *B. nuttallii* in many respects" — referring to floral features in his Table 2 — and speculated that this might reflect close common ancestry of *B. australis* and *B. nuttallii*. The phylogenetic question posed might easily be resolved with molecular data, beyond the scope of this investigation.

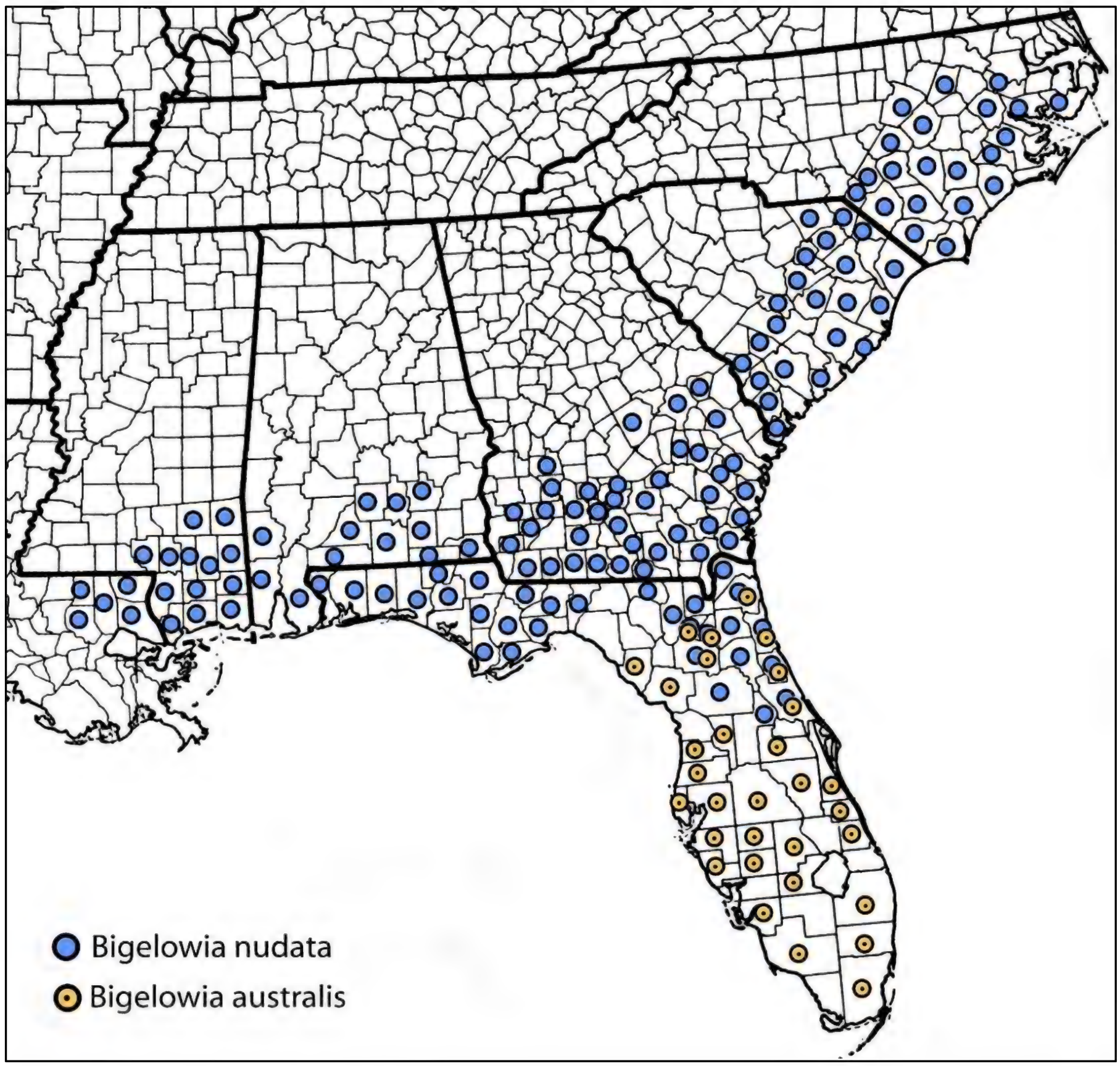

Figure 1. Distribution of *Bigelowia nudata* and *B. australis*.

***Bigelowia australis* in sympatry with *B. nudata*. Florida**. Alachua Co.: Fairbanks, cypress swamp, 3 Mar 1927 [in bud], *West 17* (FLAS). Bradford Co.: near US Hwy 301, pineland savannah, 8 Sep 1954, *Radford 8248* (NCU). Duval Co.: Baldwin, 6 Sep 1895, *Nash 2597* (US, Fig. 14). Flagler Co.: 3.4 mi W of Bunnell, along S side of Fla Hwy 100, roadside ditch in pine flatwoods, 12 Oct 1979, *Hansen et al. 6668* (USF). Union Co.: Danville, open flatwoods, 18 Aug 1939, *Murrill 773* (US, Fig. 16). Volusia Co.: Port Orange, Willow Run subdivision just E of I-95, edge of large ditch, thin pine woods with *Serenoa*, *Ilex*, *Pityopsis*, *Lyonia*, 29 Nov 1985, *Nelson 4444* (USCH). St. Johns Co.: Ca. 1.5 mi E of Sampson on Rte 210, moist roadside area, 21 Sep 1971, *Morton 4784* (USF). Collections cited above from Bradford, Duval, and Union counties were cited by Anderson (1970) as intermediates.

Figure 2. *Bigelowia nudata*. Mobile Co., Ala., *Deramus D236* (UNA).

Figure 3. *Bigelowia nudata*. Baldwin Co., Ala., *Lasseigne 15508* (LSU).

Figure 4. *Bigelowia nudata*. Geneva Co., Ala., *McDaniel 7635* (FSU).

Figure 5. *Bigelowia nudata*. Camden Co., Ga., *Carter 17352* (VSC).

Figure 6. *Bigelowia nudata*. Marion Co., Fla., *Slaughter 15,050* (USF).

Figure 7. *Bigelowia nudata*. Volusia Co., Fla., *Anderson 3480* (USF). Compare with Figs. 17 and 18, *B. australis*, also from Volusia Co.

Figure 8. *Bigelowia nudata*. Washington Co., Fla., *Anderson 3484* (GA).

Figure 9. *Bigelowia australis*. Brevard Co., Fla., *Garrett-Kraus s.n.* (PIHG).

Figure 10. *Bigelowia australis*. Levy Co., Fla., *Ford 2366* (FLAS).

Figure 11. *Bigelowia australis*. Pinellas Co., Fla., *Anderson 3471* (GA).

Figure 12. *Bigelowia australis*. Pinellas Co., Fla., *Anderson 3471* (USF).

Figure 13. *Bigelowia australis*. Polk Co., Fla., *vanHoek & Petty 691* (USF).

Figure 14. *Bigelowia australis*. Duval Co., Fla., *Nash 2597* (US).

Figure 15. *Bigelowia australis*. Flagler Co., Fla., *Hansen et al. 6668* (USF).

Figure 16. *Bigelowia australis*. Union Co., Fla., *Murrill 774* (US).

Figure 17. *Bigelowia australis*. Volusia Co., Fla., *Slaughter 13,410* (USF). Compare with Fig. 7, *B. nudata*, also from Volusia Co.

Figure 18. *Bigelowia australis*. Volusia Co., Fla., *Nelson 4444* (USCH). Compare with Fig. 7, *B. nudata*, also from Volusia Co.

Figure 19. *Bigelowia nudata*. A. St. Johns Co., Fla., 9 Nov 2018. B. Clay Co., Fla., 5 Aug 2020. C. St. Johns Co., Fla., 14 Sep 2019. D. St. Johns Co., Fla., 7 May 2020. All photos by Eric Powell, iNaturalist.

Figure 20. *Bigelowia nudata*. A. Berkeley Co., S.C., "picbor," 28 Sep 2017. B. Santa Rosa Co., Fla., Grayson Sasser, 20 Sep 2019. C. St. Johns Co., Fla., Eric Powell, 7 May 2020. D. Santa Rosa Co., Fla., Grayson Sasser, 20 Sep 2019. E. Nassau Co., Fla., Erick Powell, 3 Oct 2020. F. Harrison Co., Miss., Alison Northrup, 22 May 2020. All photos, iNaturalist.

Figure 21. *Bigelowia nudata*. Jones Co., Mississippi, 1 Aug 2018. Photo by Lillie, iNaturalist.

Figure 22. *Bigelowia nudata*. St. Johns Co., Florida. 1 Aug 2018. Photo by Eric Powell, iNaturalist. Compare with Fig. 25, *B. australis*, also from St. Johns Co.

Figure 23. *Bigelowia australis*. A. Charlotte Co., Fla., Jay Horn, 31 Oct 2019. B. Collier Co., Fla., Jay Horn, 17 Jul 2019. C. Collier Co., Fla., Jay Horn, 25 Nov 2020. D. Lee Co., Fla., gcschmidt911, 6 Sep 2020. All photos, iNaturalist.

Figure 24. *Bigelowia australis*. Charlotte Co. Florida. Photo by Jay Horn, 31 Oct 2019, iNaturalist.

Figure 25. *Bigelowia australis*. St. Johns Co., Florida. Photo by Eric Powell, 2 Aug 2017, iNaturalist. Compare with Fig. 22, *B. nudata*, also from St. Johns Co.

Figure 26. *Bigelowia australis*. Variation in caudex/rhizome structures.

Figure 27. *Bigelowia australis*. Variation in caudex/rhizome structures: left, lateral offsets from corm-like caudex; right, plants connected by short rhizomes. Photos by Alan Weakley, NCU.

Figure 28. *Bigelowia nudata*. Variation in caudex/rhizome structures.

Figure 29. *Bigelowia nudata*. Calhoun Co., Fla., *Orzell & Bridges 20749* (USF).

ACKNOWLEDGEMENTS

I'm grateful for the excellent, documented photos on iNaturalist and available through Creative Commons and for the hundreds of specimens images accessed through SERNEC and the website of the U.S. National Herbarium (US). Many thanks to Alan Weakley for comments on the manuscript.

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Nesom, G.L. 2020. *Phaseolaster*, a replacement name for *Phaseolaria* Nesom (Asteraceae). Phytoneuron 2020-93: 1.
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PHASEOLASTER, A REPLACEMENT NAME FOR *PHASEOLARIA* NESOM (ASTERACEAE)

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The recently described genus *Phaseolaria* Nesom (2020) and its three species, segregated from Australian *Olearia*, are illegitimately named because of the earlier *Phaseolaria* Printz (1921), a green alga (Chlorococcaceae). Replacement names are provided here.

PHASEOLASTER Nesom [replacement name]. *Phaseolaria* Nesom, Phytoneuron 65: 27. 2020 [not *Phaseolaria* Printz 1921]. **TYPE**: *Phaseolaria elliptica* (DC.) Nesom For Australian botanist Anthony R. Bean.

1. **Phaseolaster elliptica** (DC.) Nesom, **comb. nov.** [replacement name]. *Phaseolaria elliptica* (DC.) Nesom, Phytoneuron 65: 27. 2020. *Olearia elliptica* DC., Prodr. 5: 271. 1836.

2. **Phaseolaster fulgens** (A.R. Bean) Nesom, **comb. nov.** [replacement name]. *Phaseolaria fulgens* (A.R. Bean) Nesom, Phytoneuron 65: 27. 2020. *Olearia fulgens* A.R. Bean, Austrobaileya 10: 658. 2020.

3. **Phaseolaster praetermissa** (P.S. Green) Nesom, **comb. nov.** [replacement name]. *Phaseolaria praetermissa* (P.S. Green) Nesom, Phytoneuron 65: 27. 2020. *Olearia praetermissa* (P.S. Green) A.R. Bean, Austrobaileya 10: 660. 2020. *Oleolaria elliptica* subsp. *praetermissa* P.S. Green, Kew Bull. 48: 311. 1993.

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I'm grateful to Eduardo Antonio Molinari Novoa for pointing out the duplicate name, glad that he reads Phytoneuron so carefully and remembered details about Australian vascular plants while working on a phycological database.

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Nesom, G.L. 2020. *Chrysogonum* (Asteraceae) revisited again. Phytoneuron 2020-94: 1–28. Published 18 December 2020.
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CHRYSOGONUM (ASTERACEAE) REVISITED AGAIN

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ABSTRACT

Three species are recognized in *Chrysogonum: C. virginianum*, *C. australe,* and **Chrysogonum repens** (Cass.) Nesom, **comb. nov.** (= C. *virginianum* var. *brevistolon*). *Diotostephus repens* Cass. is neotypified. Molecular data (Nowicki et al. 2019) support the recognition of these three entities (their "Ocoee-type" corresponds to *C. repens*). A detailed distribution map of the three species is provided and reprentative specimens are shown for each.

A taxonomic summary of *Chrysogonum* L. (Nesom 2001), widely distributed through the southeastern USA (Fig. 1), recognized three entities: *C. virginianum* L. var. *virginianum*, var. *brevistolon* Nesom, and var. *australe* (Alex. ex Small) Ahles. The southernmost entity has been treated at specific rank, as *C. australe* Alex. ex Small (Weakley 2020), emphasizing its discontinuous morphology and geography. Molecular data support recognition of the three entities (Nowicki et al. 2019; and see Fig. 2 and comments below). Data of Nowicki et al. and of Schilling and Floden (2018) suggest that *C. australe* sensu stricto is the most evolutionarily distinct entity.

The original description of var. *brevistolon* noted that it is sharply delimited from var. *virginianum* by production of short stolons or rhizomes and shorter stems and that it also is contiguous and non-overlapping in geographic range, as determined at the time by both field and herbarium observations. A review reaffirms the observations of discontinuity and var. *brevistolon* is recognized here at specific rank, matching the current treatment of *C. australe* and with the same rationale.

CHRYSOGONUM REPENS (Cass.) Nesom, **comb. nov.** *Diotostephus repens* Cass. in Cuvier, Dict. Sci. Nat. 48: 544-545. 1827. *Chrysogonum diotostephus* DC., Prodr. 5: 510. 1836 (nom. illeg., replacement name for *Diotostephus repens*]. Protologue: "Nous avons fait cette description, générique et spécifique, sur un très petit ènchantillon sec, incomplet, en mauvais ètat, et dont nous ignorons l'origine." **ORIGINAL TYPE**: (P?, not seen). As noted by Stuessy (1977), Cassini's description of this taxon is explicit enough that its identity as *C. virginianum* sensu lato seems reasonable, and de Candolle, who indicated that he saw the specimen, treated it (as *C. diotostephus*) with *C. virginianum* as a second species of the genus. Cassini noted the plant produced a horizontal, hairy stolon with rooted tuft of leaves at the tip — its placement here (following Stuessy) apart from *C. australe* is based on de Candolle's description of its habitat as "in siccis pinguibus Carolinae." **NEOTYPE** (designated here): **South Carolina**. Beaufort Co.: 0.5 mi W of Gardens Corner on US Hwy 17, deciduous woods, 3 Apr 1956, *C.R. Bell 1705* (NCU, Fig. 15).

Chrysogonum virginianum var. *brevistolon* Nesom, Sida 19: 817. 2001. **TYPE**: **South Carolina**. Lexington Co.: Riverbanks Zoo Botanical Garden, old Saluda Mill site, shaded slope near ravine just S of tram line clearing, occasional herbs, somewhat trailing but with flowering stems generally erect, 7 May 1993, *J.B. Nelson 14,062* (holotype: BRIT; isotype: USCH).

The basis for recognition of *Chrysogonum repens* as a distinct entity is essentially the same as earlier (Nesom 2001; Weakley 2020) — the key below essentially repeats the one from 2001. Additional comments regarding geography and morphology are given in Nesom (2001).

1. Plants occurring individually, sometimes with short rhizomes but not with elongate stolons; earliest flowering stems leafless, later flowering stems leafy; leafy flowering stems mostly 15–35(–50) cm high; leaf blade base truncate ..... **Chrysogonum virginianum**
1. Plants colonial, stoloniferous, forming mats or interconnected colonies of individuals; flowering stems leafless or leafy; leafy flowering stems (if present) 15–25 cm high; leaf blade base cuneate.
    2. Earliest flowering stems leafless, mostly 2–10 cm high; later flowering stems leafy, 15–25 cm high; longest stolon internodes 2–6 cm long ..... **Chrysogonum repens**
    2. Earliest flowering stems leafless, 2–10 cm high; later flowering stems leafless as well, 2–10 cm high; longest stolon internodes 12–60 cm long ..... **Chrysogonum australe**

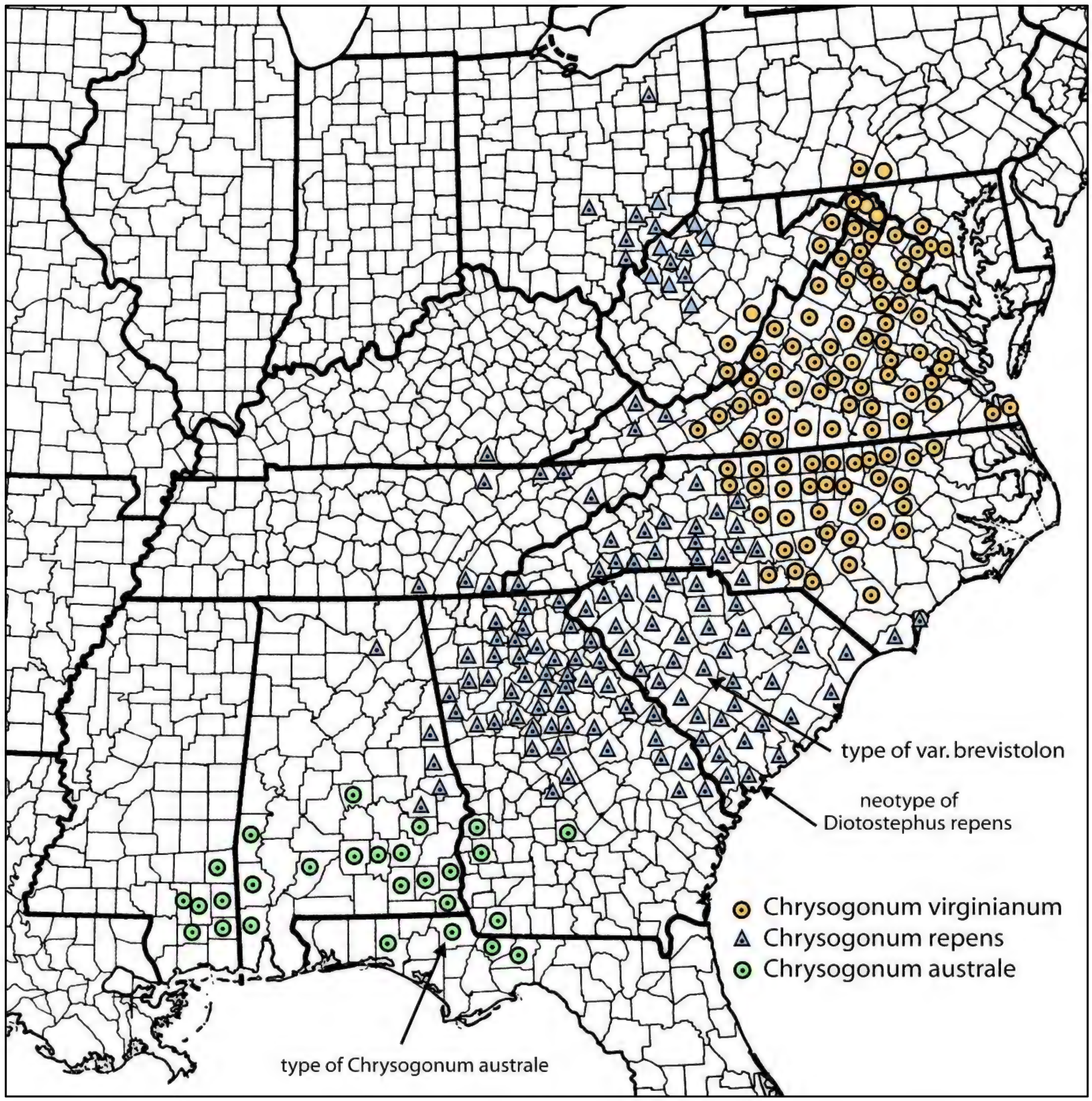

Figure 1. Distribution of *Chrysogonum* species. Based on records/images available via SERNEC and herbarium US — vouchers seen for all records except those marked by undotted symbols. A voucher cannot be located for the Louisiana occurrence (West Feliciana Parish) earlier mapped (Nesom 2001).

Nowicki et al. (2019) sought molecular characterizations of entities within *Chrysogonum*. Their clearly delimited "**virginianum**," "**australe**," and "recently discovered putative new form" "**Ocoee-type**" correspond with ***C. virginianum***, ***C. australe***, and ***C. repens*** as treated here. Their "brevistolon" (excluding the sample from Shenandoah Co., Va.; e.g., see Fig. 9) is included here within *C. repens* and presumably would include plants from southwestern Virginia, western West Virginia, and Ohio — their "brevistolon" populations (e.g., Figs. 22 and 23, from Scott Co., Tenn.) have the morphology of *C. repens* but in their analysis are not molecularly differentiated from "virginianum."

Nowicki et al. (2019) noted that their Ocoee-type has a tapering, cuneate leaf base similar to var. *australe* but lacks its distinctive stolons. Among their cited samples of the Ocoee-type, however, all plants that I have seen produce stolons and are indistiguishable from var. *brevistolon* = *C. repens* (Kral collections from McDuffie, Dawson, and Lumpkin cos., Ga. (VDB images!); *Floden 2879* (APSC image!) and *2880* (APSC, Fig. 24) from Polk Co., Tenn. Various other collections from Polk Co. are similar — *Pistrang s.n.* (TENN, Fig. 26), *Williams 1573* (UCHT image!), *Wilson 85* (MTSU image!), and three collections by *Shaw et al. s.n.* (APSC images!, e.g., Fig. 25).

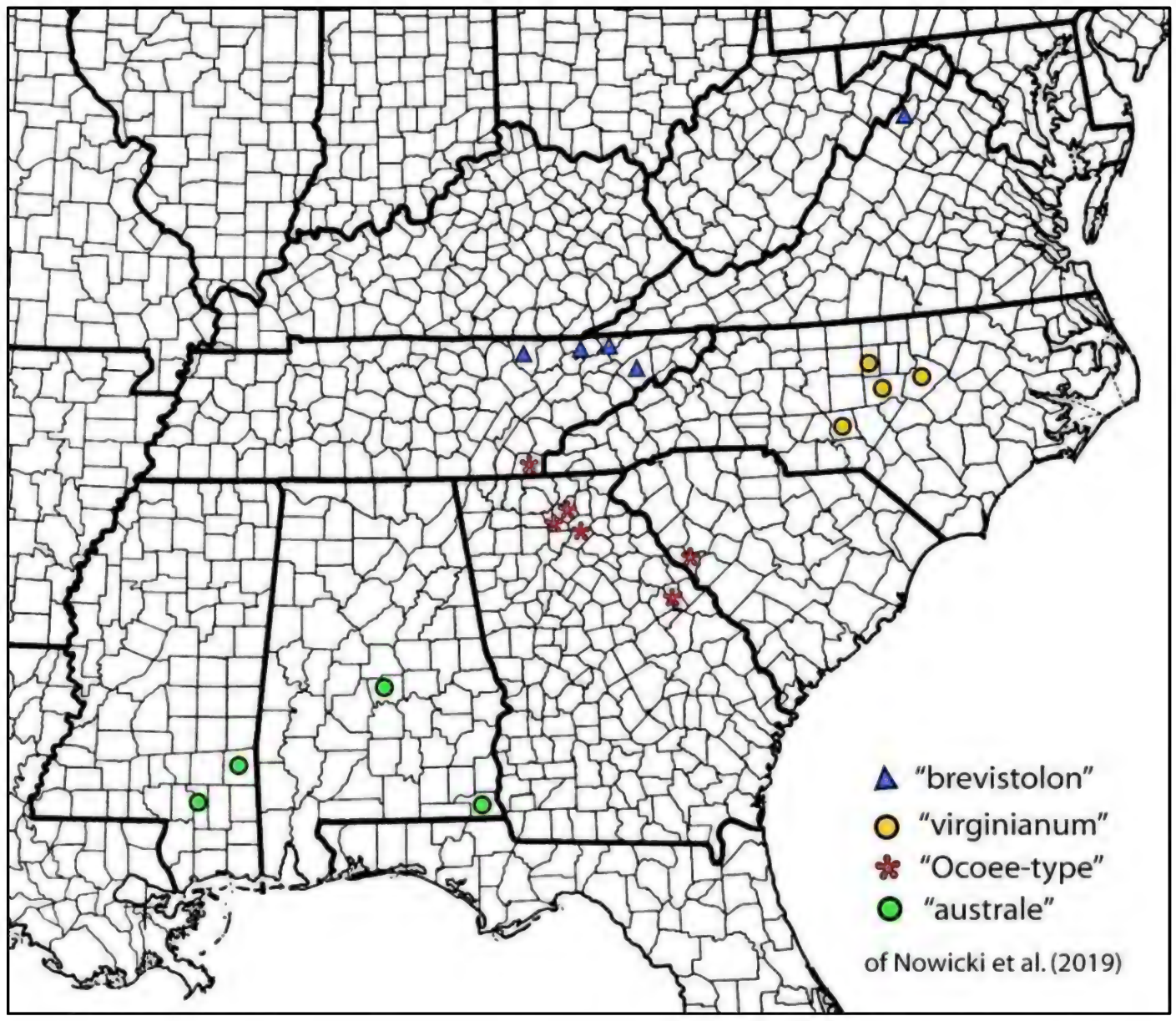

Figure 2. Distribution of the molecular entities within *Chrysogonum* found by Nowicki et al. (2019), as mapped from data in their Table 1.

In contrast to my earlier identifications, the range of *Chrysogonum repens* is recognized here to extend from northeastern Tennessee (eg., Figs. 22 and 23) into West Virginia (e.g., Figs. 20 and 21) and Ohio. Data of Nowicki et al. (2019) indicate that this population system is molecularly undifferentiated from typical *C. virginianum* (their samples from central North Carolina), in contrast to typical *C. repens* (their samples from Georgia and South Carolina), which is molecularly distinct from both *C. virginianum* and *C. australe*. I have not found a corresponding morphological difference between northern and southern systems of *C. repens* but more detailed study should apply. If the molecular differentiation is confirmed, the two systems perhaps originated independently or the northern may be involved in the evolutionary parentage of the southern.

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 3. *Chrysogonum australe*. Jackson, Co., Florida. Holotype: *R.L. Harper s.n.* (NY).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 4. *Chrysogonum australe*. Jackson, Co., Florida, *Gholson 408* (FLAS).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 5. *Chrysogonum australe*. Jackson, Co., Florida, *Godfrey 78745* (TTRS).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 6. *Chrysogonum australe*. Stewart Co., Georgia, *Allison 3050* (GA).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

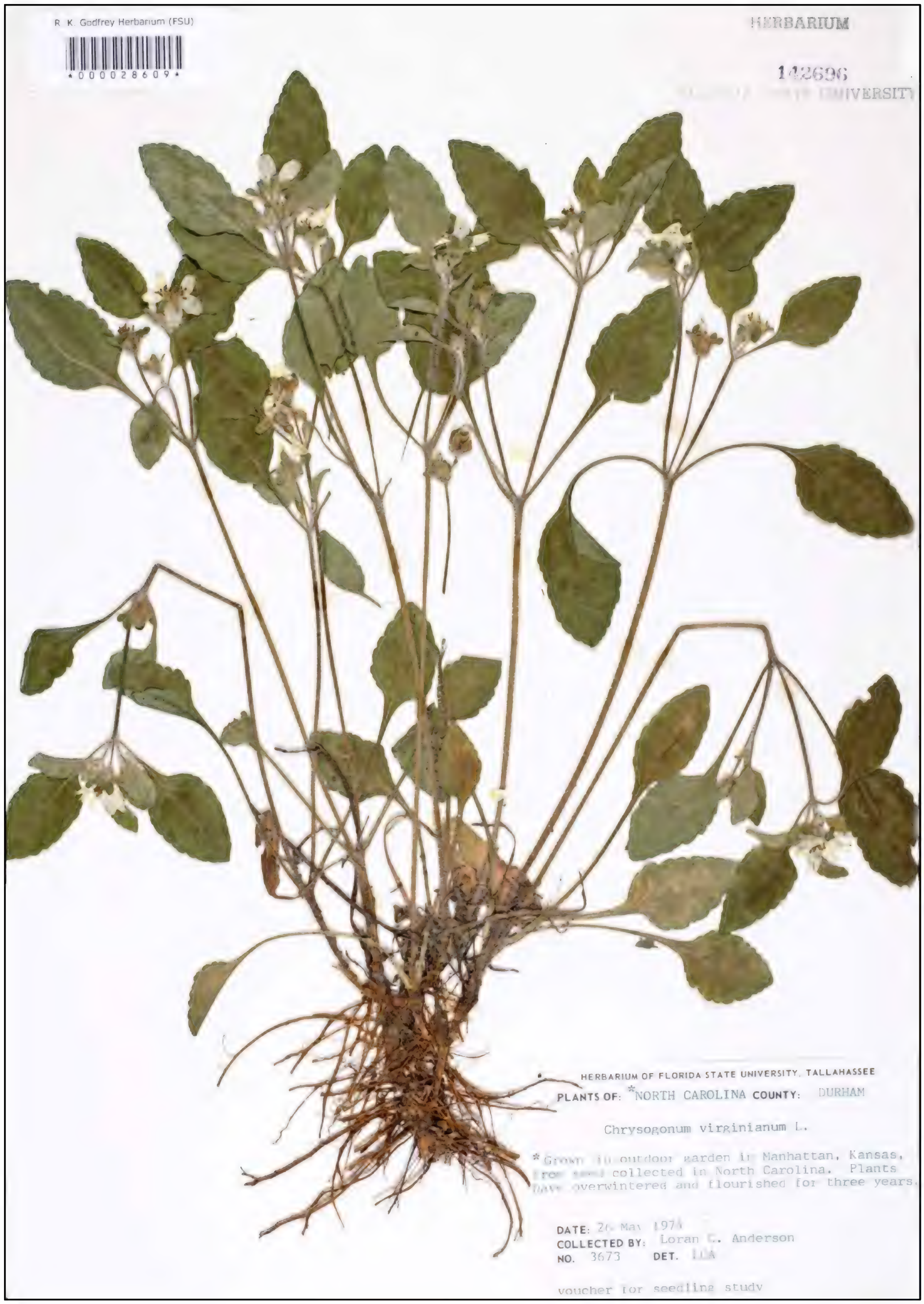

Figure 7. *Chrysogonum virginianum*. Durham Co., North Carolina, *Anderson 3673* (FSU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 8. *Chrysogonum virginianum*. Orange Co., North Carolina, *Levesque 193* (NCU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 9. *Chrysogonum virginianum*. Shenandoah Co., Virginia, *Allard 4636* (VPI).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 10. *Chrysogonum virginianum*. Hardy Co., West Virginia, *Cusick 23,551* (NCU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 11. *Chrysogonum virginianum*. Chatham Co., North Carolina, *Massey 3209* (NCU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 12. *Chrysogonum virginianum*. Orange Co., North Carolina, *Edwards & Johnson 25* (NCU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

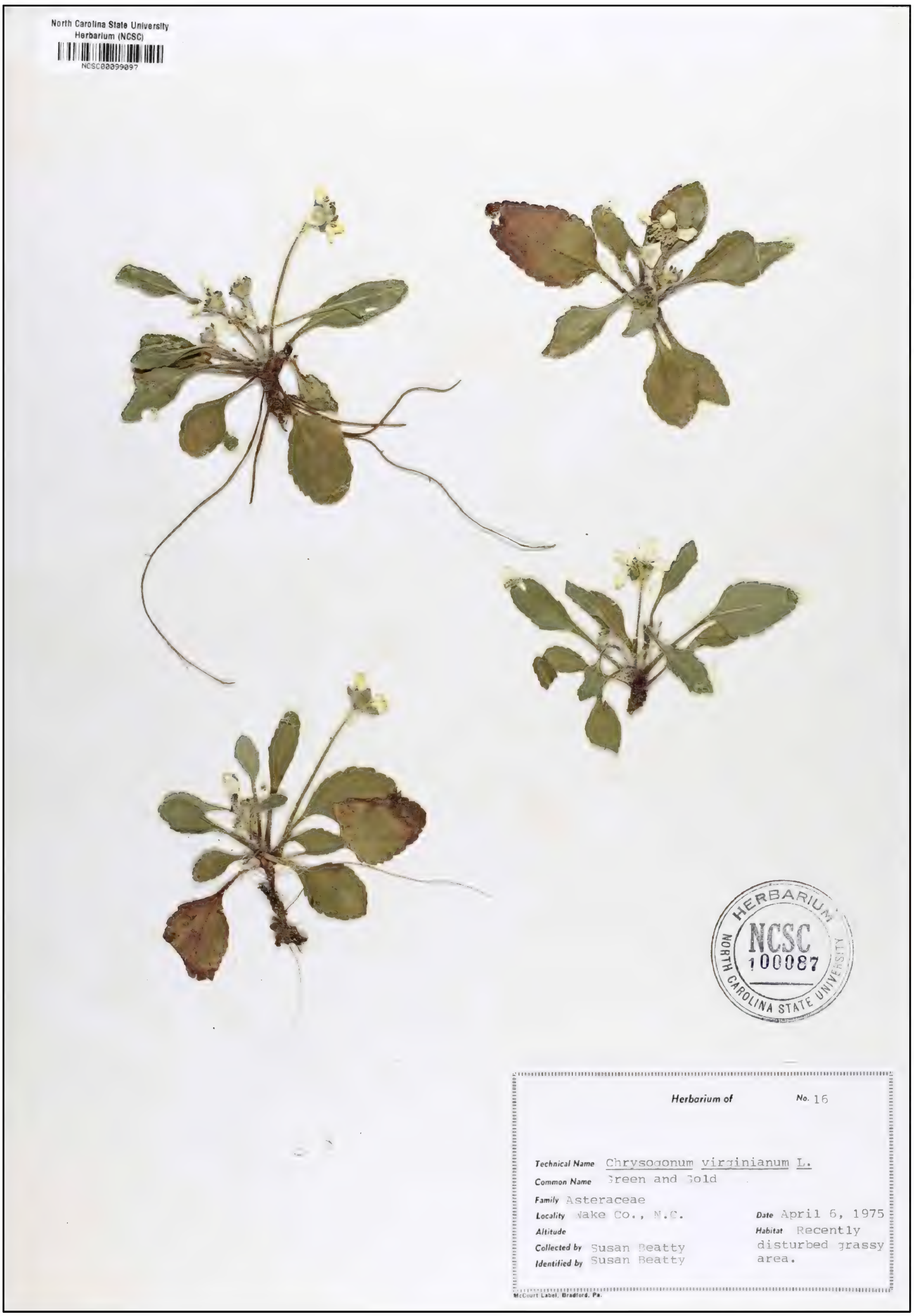

Figure 13. *Chrysogonum virginianum*. Wake Co., North Carolina, *Beatty 16* (NCSC). Juvenile form, with scapose peduncles.

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 14. *Chrysogonum repens*. Berkeley Co., South Carolina, *Nelson 25776* (USCH).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 15. *Chrysogonum repens*. Beaufort Co., South Carolina. Neotype of *Diotostephus repens*, *Bell 1705* (NCU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 16. *Chrysogonum repens*. Colleton Co., South Carolina, *Woodward 18* (CLEMS).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 17. *Chrysogonum repens*. Effingham Co., Georgia, *Hardin 15150* (GA).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 18. *Chrysogonum repens*. Lumpkin Co., Georgia, *Kruse 01-59b* (GA). Juvenile form, with scapose peduncles.

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 19. *Chrysogonum repens*. DeKalb Co., Georgia, *Moore 1914* (GA). Juvenile form.

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 20. *Chrysogonum repens*. Ritchie Co., West Virginia, *Cusick 24,196* (NCU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 21. *Chrysogonum repens*. Wirt Co., West Virginia, *Bartholomew W1941-1034* (GAS).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 22. *Chrysogonum repens*. Scott Co., Tennessee, *Panero 695* (TENN).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 23. *Chrysogonum repens*. Scott Co., Tennessee, *Goodson 994* (HTTU).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 24. *Chrysogonum repens*. Polk Co., Tennessee, *Floden 2880* (APSC). Cited by Nowicki et al. (2019) as "Ocoee-type."

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 25. *Chrysogonum repens*. Polk Co., Tennessee, *Shaw s.n., 11 May 2011* (APSC).

Nesom: *Chrysogonum repens* = *C. virginianum* var. *brevistolon*

Figure 26. *Chrysogonum repens*. Polk Co., Tennessee, *Pistrang s.n.* (TENN).

ACKNOWLEDGEMENTS

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